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Trophic impact of large predators on coral reefs and management implications

Thesis submitted by

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Statement on the Contribution of Others

This thesis includes collaborative work with my supervisors Prof. Mark McCormick, Dr. Ashley Frisch, Dr. Andrew Hoey and other colleagues. While undertaking these collaborations, I was responsible for the project concept and design, data collection, analysis and interpretation, and the final synthesis of results into a form suitable for publication. My collaborators provided technical assistance, equipment, intellectual guidance, editorial assistance and financial support. Aside from standardised formatting for the thesis, all data chapters have been presented as published

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GENERAL ABSTRACT

Apex predators such as lions, wolves and orcas occupy the top of food chains and are known to exert strong top-down control of prey abundance, community structure and ecosystem productivity. Despite the importance of apex predators in both terrestrial and oceanic habitats, there is a paucity of information on this guild for coral reef ecosystems. Sharks are among the largest predators on coral reefs and may function as apex predators, but our understanding of the ecological role and importance of these organisms is poor. Recent declines in shark populations are also leading to concerns that these potentially important species may be effectively lost from reef systems before we realise their role in ecosystem dynamics. Thus, the overall focus of this thesis was to examine the status, trophic role and importance of large predators, namely reef sharks, on coral reefs, thereby providing management with improved tools for understanding how the removal of predators via fishing influences ecosystem properties.

The high mobility and generally low abundances of reef sharks has led to considerable debate regarding the optimal method/s for assessing their population status. Due to controversy surrounding previous stock assessments, the focus of ***Chapter 2*** was to evaluate potential biases in five survey methods (timed-swim, towed-diver, baited-remote-underwater-video, stationary-point-count, and audible-stationary-count) for assessing reef shark populations, and whether these biases (if any) vary among reefs that are subject to different levels of human interaction due to conservation zoning. For timed-swim, towed-diver, and baited-remote-underwater-video (BRUV) surveys, shark encounter rates were constant over time, suggesting minimal bias caused by, for example, shark attraction to divers. For audible-stationary-count (ASC) surveys, encounter rates were elevated initially, then decreased rapidly, but the extent of upward bias did not differ between management

zones. Timed-swim, BRUV, and ASC surveys produced comparable estimates of shark density, however, towed-diver-surveys produced significantly lower estimates of shark density. These findings provide no evidence for biases in diver-surveys: encounter rates with sharks were not elevated when divers first entered the water; behavioural responses of sharks were consistent across management zones; and diver-surveys yielded abundance estimates comparable to stationary non-diver surveys. These results indicate that estimates of abundance generated by diver-surveys such as underwater visual transects are reliable, minimally biased, and suitable for assessing shark populations in the field.

Quantifying the distribution and habitat use of sharks is critical for estimating their population sizes, understanding their ecological role, and for establishing appropriate conservation and management regimes. The goal of ***Chapter 3*** was to survey shark populations across outer-shelf reefs of the Great Barrier Reef (GBR) in order to determine the diversity, abundance, and distribution of reef sharks across three major coral reef habitats: (1) the reef slope, (2) the back reef and (3) the reef flat. Results revealed that, of the variables that were examined, habitat was the best predictor of shark distribution and abundance. Specifically, overall shark abundance and diversity were significantly higher on the reef slope (and to a lesser degree, the back reef) than the reef flat. These results confirm that shark populations are not homogeneously distributed across coral reefs and also highlight the potential importance of the reef slope, with high levels of live coral cover, structural complexity, and diversity of potential prey species for sustaining reef shark populations.

The goal of ***Chapter 4*** was to examine the top-down influence of reef sharks and mesopredators (predatory teleost fishes) on herbivores across a large spatial gradient. The abundance, size structure, and biomass of apex predators, mesopredators, and herbivores across fished, no-take, and no-entry management zones of the GBR were estimated. Shark abundance and mesopredator size and biomass were higher in no-entry zones than in fished and no-take zones, which indicates the viability of strictly enforced human exclusion areas as tools for the conservation of predator communities. However, changes in predator populations due to protection in no-entry zones did not have a discernible influence on the density, size, or biomass of different functional groups of herbivorous fishes. The lack of a relationship between predators and herbivores suggests that top-down forces may be much weaker than previously thought and that food web models developed for terrestrial systems may not be appropriate for describing reef communities across large spatial scales.

Using life-like models of a reef shark and another large predatory fish (coral-grouper), ***Chapter 5*** examined the indirect effects of large predators on herbivore foraging behaviour and algal consumption. This study found that the presence of a model blacktip reef shark (1.7m length) or large coral-grouper (76 cm length) led to a substantial reduction in bite rate and species richness of herbivorous fishes feeding on a macroalgal thallus in the vicinity of the predator. The perceived risk of predation led to a near absolute localized cessation of macroagal removal. A smaller-sized model coral-grouper (48 cm length) also reduced herbivore diversity and activity but to a lesser degree than the larger model predators. These results highlight that the indirect effects of large predators on the foraging behaviour of herbivores may have flow-on effects on the biomass and distribution of macroalgae on a localized scale. Combined with the results of Chapter 4, this highlights that the ecological interactions and processes that contribute to ecosystem resilience may be more complex than previously assumed.

Due to their large size and conspicuous predatory behaviour, reef sharks are typically assumed to be apex predators on coral reefs, but this title is tenuous because little is known about their trophic ecology and functional role. In ***Chapter 6*** stomach contents and stable isotope ratios (δ^{13}Carbon and δ^{15}Nitrogen) were used to estimate diet, trophic level and sources of primary production of three reef sharks (*Triaenodon obesus*, *Carcharhinus*

melanopterus and *Carcharhinus amblyrhynchos*) from the GBR. Their assumed functional roles as apex predators were evaluated by qualitative and quantitative comparisons with other sharks and large predatory fishes. It was found that reef sharks do not occupy the apex of coral reef food chains, but instead appear to have functional roles similar to those of large predatory fishes, which are typically regarded as high-level mesopredators. These findings suggest that a high degree of functional redundancy may exist within this guild of large predators, potentially explaining why shark-induced trophic cascades are rare or subtle in coral reef ecosystems. Furthermore, these results indicate that reef sharks should be reassigned to an alternative trophic group such as mesopredators. This change will increase the accuracy of ecosystem models, providing resource managers with improved tools for understanding how reef communities function and how removal of predators might affect ecosystem properties.

The current body of work has advanced our understanding of reef sharks, particularly in terms of their response to protection from fishing, spatial distribution, behaviour towards divers and their functional roles on coral reefs. This thesis demonstrates that reef sharks respond positively to protection from fishing but that the flow-on effects to lower trophic levels are variable and inconsistent with theory surrounding trophic cascades. These advances will be important for improving ecosystem-based management strategies that aim to conserve not only individual species, but also their functions and interactions. Such an approach is paramount given that coral reefs around the globe face ever-intensifying human-induced threats such as overfishing and climate change.

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CHAPTER 1: General Introduction

Predation can play a vital role regulating prey populations and in shaping ecological communities (Paine 1966; Hixon et al. 2002). In particular, changes in the density and distribution of large-bodied predators, otherwise referred to as apex predators, can exert strong top-down ecological effects that cascade through an entire ecosystem (Estes et al. 1998, 2011; Ripple et al. 2001, 2014; Frank 2008; Sandin et al. 2008). Apex predators can be defined as species that occupy the top trophic position in a community, and have few to no predators of their own (Ritchie and Johnson 2009). Apex predators are typically characterized by *K*-selected life history traits, such as slow growth rates, late sexual maturity, and low fecundity, and are often preferentially targeted by humans for food or game (Pauly et al. 1998; Myers and Worm 2003). Consequently, apex predators are often the first to become extinct or locally extirpated.

Globally, apex predators are experiencing rapid declines in their populations and geographic ranges, largely as a result of exploitation by humans and habitat degradation (Treves and Karanth 2003; Dulvy et al. 2014; Ripple et al. 2014). For example, a recent global synthesis describing the conservation status of the 31 largest mammalian predators indicates that over half (61%) are listed by the International Union for the Conservation of Nature (IUCN) as threatened (Ripple et al. 2014). This is worrisome because apex predators often exert extensive top-down control with substantial flow-on effects to the structure and function of entire ecosystems (Estes et al. 2011; Ripple et al. 2014). Evidence of this comes from both aquatic and terrestrial systems. For example, in the northern Pacific ocean killer whale predation on sea otter populations have led to increased sea urchin density and subsequent declines of habitat-forming kelp beds (Estes et al. 1998). In Yellowstone National Park, a long-term research program on the ecological impact of grey wolf (*Canis lupus*) loss and subsequent recovery has revealed that these apex predators can indirectly influence the spatial distribution woody plant species by altering the abundance and/or behaviour of herbivorous elk (*Cervus elaphus*) (Ripple et al. 2001; Ripple and Beschta 2012). Plants, such as trees and kelp, provide the primary production and habitat structure in these systems and as such any reductions or losses can have major effects on the biodiversity and functioning of the entire ecosystems (Fortin et al. 2005; Estes et al. 2011; Letnic et al. 2012; Ripple et al. 2013). Thus, the maintenance of healthy apex predator populations may contribute to biodiversity conservation (Sergio et al. 2006) and ecological stability (Ritchie et al. 2012). Although a popular topic for investigation (Estes et al. 2011; Ripple et al. 2014; Sergio et al. 2014), our understanding of the roles played by apex predators is still limited, particularly in the marine realm.

Sharks are commonly regarded as apex predators in marine ecosystems (Heithaus et al. 2008; Rizzari et al. 2014a) but their populations are rapidly declining due to the combination of intense fishing pressure, habitat degradation and their conservative life-history traits (Dulvy et al. 2014; Rizzari et al. 2014b). This is worrisome because altering the density of sharks may invoke community-wide trophic cascades that have far-reaching, detrimental consequences for fisheries resources and the human livelihoods that depend on them (Myers et al. 2007; Heithaus et al. 2008). In some marine systems, such as coral reefs, apex predator induced trophic cascades may have a similar function (Bascompte et al. 2005; Ruppert et al. 2013), but evidence is circumstantial. Therefore, a better understanding of the role and importance of apex predators is an important consideration for ecosystem management.

Coral reefs are one of the world’s most taxonomically diverse ecosystems, harboring approximately 5,000 species of fishes that perform numerous functions and create a complex network of species interactions (Sheppard et al. 2009). However, coral reefs are in global decline due to both natural and human-induced disturbances (Pandolfi et al. 2003; De'Ath et al. 2013). Overfishing has played a major role in contributing to the observed decline of coral reefs and associated fish populations (Jackson et al. 2001), particularly apex predators such as reef sharks (Friedlander and DeMartini 2002, Robbins et al. 2006; Nadon et al. 2012). Recent surveys of sharks of the Red Sea (Berumen et al. 2013), the Great Barrier Reef (Robbins et al. 2006; Hisano et al. 2011), the Indian Ocean (Graham et al. 2010), the Pacific Ocean (Nadon et al. 2012) and the Caribbean (Ward-Paige et al. 2010b) indicate substantial declines compared to estimated baseline populations, which have been primarily attributed to increased fishing pressure. It is possible, therefore, that reef sharks may be lost from coral reef ecosystems before we fully understand their ecological roles or the consequences of their removal (Ceccarelli et al. 2014).

Three species of reef sharks that are most often found on or near coral reefs are the whitetip reef shark (*Triaenodon obesus*) the blacktip reef shark (*Carcharhinus melanopterus*) and the grey reef shark (*Carcharhinus amblyrhynchos*), and are therefore the focal species for this thesis (Fig. 1.1). Reef sharks have a strong affinity for reefs with high coral cover and structural complexity (Espinoza et al. 2014; Rizzari et al. 2014c), presumably because these reefs provide the necessary habitat requirements and/or food resources. However, the contribution of reef sharks to the well being of coral reef ecosystems is unclear, but is potentially important (Heithaus et al. 2008; Ruppert et al. 2013).

The effect of reef sharks on lower trophic levels, particularly herbivorous fish assemblages, is particularly important for coral reef managers. Herbivores perform a critical role on coral reefs by mediating the competition for space between corals and algae. Accordingly, declining herbivorous fish populations have resulted in the expansion of macroalgae in many reef systems (Hughes et al. 2007b; Rasher et al. 2013). While declines in herbivory have been linked to overfishing of herbivores themselves (Hughes et al. 2007a), similar responses may also manifest through changes in predator communities (Houk and Musburger 2013; Ruppert et al. 2013; Rizzari et al. 2014a). However, outputs of theoretical models provide contrasting evidence as to whether reef sharks play a major (Bascompte et al. 2005) or minor (Stevens et al. 2000) role in trophic structuring on coral reefs. Thus, a better understanding of reef sharks and their ecological role is imperative for guiding management actions that aim to preserve or enhance ecosystem resilience.

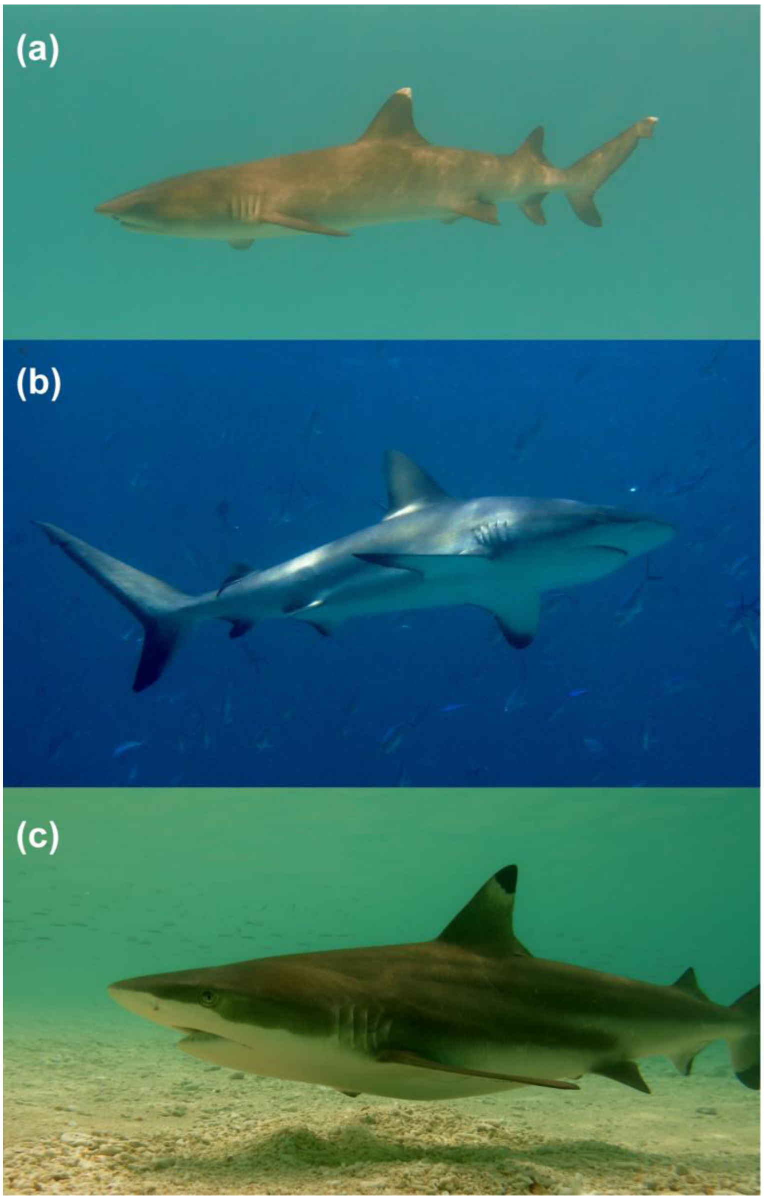

Fig. 1.1. Reef shark species. (a) whitetip reef shark, *Triaenodon obesus*, (b) grey reef shark, *Carcharhinus amblyrhinchos*, and (c) blacktip reef shark, *Carcharhinus melanopterus*. Photographs by author.

Accurately quantifying the ecological role of reef sharks is however impeded by the current lack of knowledge surrounding two basic, but critical, ecological components: (1) accurate population assessments and (2) reef shark habitat distribution. Firstly, the severity of reef shark population declines (Robbins et al. 2006; Heupel et al. 2011) is the subject of debate (e.g. Heupel et al. 2009), with differences in survey method selection commonly cited as a potential cause of bias in abundance estimates (Graham et al. 2010; Ward-Paige et al. 2010a; Ruppert et al. 2013). Sharks may respond variably to different stimuli such as noise, bait, divers and boats (Ward-Paige et al. 20120a; Cubero-Pardo et al. 2011; Fitzpatrick et al. 2011). Further, some methods, particularly diver-based abundance counts, have been criticized for potentially producing biased estimates of differences in shark abundance across gradients of protection from fishing and human interaction (Ward-Paige et al. 2010a). This is based on the hypothesis that if sharks are less accustomed to people at unfished or remote locations, they may be more likely to approach divers, leading to over-estimates of abundance in those locations, relative to areas with more human activity (Graham et al. 2010). Secondly, the distribution of reef sharks across major reef habitat types is still yet to be quantified, particularly on the Great Barrier Reef (GBR). Recent surveys on the GBR have reported alarmingly low numbers of reefs sharks (Robbins et al. 2006; Ayling and Choat 2008; Hisano et al. 2011). However, these reports were based on surveys that were confined to a single habitat, the seaward reef slope, but no surveys were conducted on other reef habitats, such as the back reef or reef flat. Sharks often have complex movement patterns within coral reef ecosystems, which makes it difficult to interpret their habitat use (Pikitch et al. 2005; Heupel et al. 2009; Heupel et al. 2010; Chin et al. 2012). Recent tracking studies using acoustic telemetry have provided insight into general habitat use patterns of reef sharks, with most shark detections occurring adjacent to the reef slope (e.g. Field et al. 2011; Barnett et al. 2012; Heupel and Simpfendorder 2014). However, fine-scale patterns in reef shark distributions across major reef habitats are still poorly understood (see Dale et al. 2011 for exception). Before we can begin to understand the trophic roles played by reef sharks, or establish appropriate conservation and management regimes, we must first determine if any biases exist in population assessments of reef sharks, and quantify reef shark distribution and habitat use patterns.

Study system

Effective marine reserves can protect reef shark populations (Robbins et al. 2006; Heupel et al. 2009) and are increasingly advocated for fisheries management, conservation, and enhancing key ecosystem processes (Graham et al. 2011; McClanahan et al. 2014). As such, marine reserves can be used as reference areas to quantify the detrimental effects of human activities, such as fishing (Graham et al. 2011). The management zoning system of the Great Barrier Reef Marine Park (GBRMP) provides an ideal setting in which to investigate the role of reef sharks because it generates strong gradients in fishing pressure, which demonstrably influence predator populations (Robbins et al. 2006). The management system of the GBRMP includes no-entry zones, which are strictly enforced human exclusion areas; no-take zones, which are conservation areas where fishing is prohibited but non-extractive activities (e.g. diving) are allowed; and fished zones, which are general use areas permitting fishing and other extractive activities (Fernandes et al. 2005). Finally, herbivorous fishes are not typically targeted by fishers on the GBR and as such the GBR harbors a relatively intact herbivore community (Done 1982; Newman et al. 1997; Frisch et al. 2014). Thus, the GBR presents a unique opportunity to examine the effects of top-down trophic structuring of reef sharks with minimal confounding effects.

Aims and thesis outline

Given the debate surrounding the current status of reef shark populations, particularly on the GBR, and our lack of understanding regarding the role that reef sharks play in coral reef ecosystem function, the main objective of this thesis was to investigate the status and functional role of reef shark populations. Using the GBR, the largest reef system in the world, as a model system the primary aims of this study were to: (1) determine a suitable method for assessing reef shark populations across different management zones; (2) quantify variation in reef shark abundance, diversity, and distribution across major reef habitat types; (3) investigate the influence of reef sharks on lower trophic levels, with a focus on herbivorous fishes, across distinct spatial scales: (a) large-scale influence of reef sharks on herbivore populations and (b) small-scale influence of a reef sharks and other large predators on herbivore foraging behaviour and algal consumption; and (4) examine the traditionally defined role of reef sharks as apex predators on coral reefs through dietary analysis.

These aims are addressed in a series of five separate studies (one per chapter, as outlined below) and correspond directly to the publications derived from this thesis (see Appendix A for full list). Accurate survey methods are needed for population assessments and to investigate how a particular guild of predators influences trophic interactions. Accordingly, ***Chapter 2*** provides an assessment of different survey techniques for quantifying reef shark abundance. The different survey techniques are performed across a gradient of protection from fishing, which generate a gradient of human interaction, to examine how human presence (or absence) impact reef shark population assessments. ***Chapter 3*** investigates the abundance, diversity and distribution of reef sharks across major reef habitat types on outer-shelf reefs of the GBR (i.e. reef flat, back reef, and reef slope). ***Chapter 4*** builds on Chapters 2 and 3 by using the most suitable survey method to assess the large-scale influence of reef sharks on lower trophic levels, namely herbivorous fishes. The principal habitat surveyed was the reef slope, as this habitat was determined to harbor the greatest abundance and diversity of reef sharks (Chapter 3). Surveys were performed across a large-spatial gradient of the GBR encompassing a total of 18 reefs with six reefs per management zone (fished, no-take, and no-entry). ***Chapter 5*** examines the small-scale (localized) influence of reef shark (and other large predator) presence on herbivore foraging behaviour and algal consumption. Model predators and stationary underwater video cameras were used to directly quantify how herbivores respond to the visual threat of a potential predator and how this directly relates to the removal of macroalgal biomass. Finally, ***Chapter 6*** uses a combination of stomach contents and stable isotope analysis to infer diet of reef sharks on the GBR. The summation of this information is used to reassess the traditionally defined functional role of reef sharks as “apex predators” on coral reefs.

CHAPTER 2: How robust are estimates of coral reef shark depletion?

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2.1 Synopsis

On coral reefs, diver-surveys of shark abundance indicate that populations are severely depleted, even in no-take zones with low levels of illegal fishing, but are protected by strictly enforced no-entry zones. These findings have been questioned, on the grounds that diver-surveys overestimate shark abundance. We evaluated whether divers encounter sharks at higher rates when they first enter the water, and whether these effects vary among reefs that are subject to different levels of human interaction due to management zoning. We also examined the consistency of abundance estimates derived from multiple survey methods. For timed-swim, towed-diver, and baited-remote-underwater-video (BRUV) surveys, encounter rates were constant over time. For audible-stationary-count (ASC) surveys, encounter rates were elevated initially, then decreased rapidly, but the extent of upward bias did not differ between management zones. Timed-swim, BRUV, and ASC surveys produced comparable estimates of shark density, however, towed-diver-surveys produced significantly lower estimates of shark density. Our findings provide no evidence for biases in diver-surveys: encounter rates with sharks were not elevated when divers first entered the water; behavioural responses of sharks were consistent across management zones; and diver-surveys yielded abundance estimates comparable to other stationary methods. Previous studies using underwater counts have concluded that sharks are vulnerable to low levels of illegal fishing in no-take management zones, and that additional measures are needed to protect species, which, like sharks, have demographic characteristics that make them vulnerable to low levels of exploitation. Our results support the robustness of the abundance estimates on which those conclusions have been based.

2.2 Introduction

Apex predators are large carnivores that occupy the top trophic level of food webs. They are typically characterized by conservative life history traits, such as slow growth rates, late sexual maturity, and low fecundity. These traits make them particularly susceptible to over-harvesting, and apex predators often are preferentially targeted by humans for food or game (e.g. Myers and Worm 2003). Consequently, apex predators are typically the first to become extinct or locally extirpated. This loss of apex predators may have extensive, adverse effects on ecosystem structure and function. In terrestrial, marine and freshwater systems, for example, changes in apex predator abundance have affected herbivore populations, with substantial flow-on effects to plant communities that provide the primary production and habitat structure that support biodiversity in these ecosystems (Estes et al. 2011).

In marine food webs, sharks are common apex predators, and also are socio-economically valuable resources (Heithaus et al. 2008). This is most apparent in tropical ecosystems, such as coral reefs, where reef sharks are believed to play an important role in ecosystem resilience (e.g. Ruppert et al. 2013), and they generate ~$1billion USD annually from ecotourism and fisheries (Cisneros-Montemayor et al. 2013). However, recent surveys of sharks of the Red Sea (Berumen et al. 2013), the Great Barrier Reef (GBR; Robbins et al. 2006; Hisano et al. 2011), the Indian Ocean (Graham et al. 2010), the Pacific Ocean (Nadon et al. 2012) and the Caribbean (Ward-Paige et al. 2010b) indicate substantial declines compared to estimated baseline populations, which have been primarily attributed to increased fishing pressure. Given the putative ecosystem functions provided by sharks, the need for accurate assessments of population status is crucial for effective coral reef management and to sustain the livelihoods of people who depend on their ecosystem goods and services.

Currently, the severity of shark population declines on coral reefs is disputed (e.g. Heupel et al. 2009). Differences in survey method selection are commonly cited as a potential cause for discrepancies in abundance estimates (e.g. Graham et al. 2010; Ward-Paige et al. 2010a; Ruppert et al. 2013). Sharks may respond variably to different stimuli such as noise, bait, divers, and boats, which are employed in different ways in different types of surveys (Ward-Paige et al. 2010a; Cuber-Pardo et al. 2011; Fitzpatrick et al. 2011). In addition, some methods, particularly diver-based counts, have been criticized for potentially producing biased estimates of differences in shark abundance along gradients of human interaction (Ward-Paige et al. 2010a). If sharks are less accustomed to people at unfished or remote locations, they may be more likely to approach divers, leading to over-estimates of abundance in those locations, relative to areas with more human activity (Graham et al. 2010).

Recent studies have concluded that reef shark populations in fished areas are severely depleted, and that low levels of poaching render no-take marine reserves much less effective than strictly enforced no-entry zones (Robbins et al. 2006; Ayling and Choat, 2008). Because estimates of population status in these studies have relied heavily on relative abundances from diver-based surveys, resolving the controversy about the validity of these approaches is crucial for evaluating the effectiveness of no-take marine protected areas for protecting apex predators with low intrinsic population growth rates, such as reef sharks, and for determining how best to assess the status of such populations. In particular, for estimates of baseline shark densities to be unbiased, sharks should neither actively avoid, nor approach, divers conducting surveys. Consequently, estimates of population depletion based on relative abundances estimated in fished and unfished areas, will be compromised if any such biases differ in magnitude in areas with different levels of fishing pressure. To date, the only study to investigate the performance of survey methods for sharks was undertaken at a single remote location (Palmyra Atoll, Line Islands) where sharks may be naïve towards humans (McCauley et al. 2012). Thus, an assessment of sharks' responses to alternative survey methods across a gradient of human interaction, and the responses' implications for estimates of absolute and relative abundance, is needed to assess the robustness of recent conclusions about the status of reef shark populations and their vulnerability to poaching in no-take marine reserves.

Here, we address this issue by comparatively evaluating four visual survey techniques that are commonly used for estimating shark abundance: (1) timed-swim, (2) towed-diver, (3) stationary-point-count (SPC), and (4) baited-remote-underwater-video (BRUV). In addition, we trialed a novel survey method, (5) audible-stationary-count (ASC), which uses low frequency sound to attract sharks to a stationary point. During each replicate survey, we recorded any observed behavioural response of sharks to divers, as well as the time at which each shark was observed. If sharks are attracted to divers, then we expect encounter rates with new individuals to be high when divers first enter the water to commence counting, and to decrease thereafter. Conversely, if sharks respond neutrally to divers, encounter rates should not increase or decrease over the course of a survey time. Each method was repeated across a gradient of human interaction in order to quantify whether any such biases vary, depending on the prevalence of human activity on the reef. To achieve this, we conducted our study in the Great Barrier Reef Marine Park (GBRMP), a system of spatial zoning that includes: (1) no-entry zones, which are strictly enforced exclusion areas; (2) no-take zones, which are conservation areas where fishing is prohibited, but non-extractive activities (e.g. diving) are allowed and where low levels of illegal fishing have been recorded (Davis et al. 2004); and (3) fished zones, which are general use areas that allow fishing and other extractive activities. Finally, we converted all shark counts to density estimates, and we tested for any differences between survey methods in shark abundance estimates, allowing for potential interactive effects with management zone and habitat type.

2.3 Methods

Study sites and species

Surveys were performed at Rib Reef (fished zone), Little Kelso Reef (no-take zone) and Bandjin Reef (no-entry zone) in the central Great Barrier Reef (GBR), and Northwest Reef (fished zone), Tryon Reef (no-take zone) and Wreck Reef (no-entry zone) in the southern GBR (Fig. 2.1). At each reef, zone boundaries are a minimum of 1-2 km from the reef edge. All six reefs are comparable in morphology and distance from shore, with a well-developed reef slope, reef flat and back reef, and each reef has an intact faunal community that is typical of reefs in the GBR (Done 1982; Newman et al. 1997; Frisch et al. 2014). More than 4,000 recreational vessels, >200 commercial line-fishing vessels and dozens of dive-charter vessels operate in the central and southern GBR (Lunow and Holmes 2011; Taylor et al. 2012). During the course of this study, up to ten boats were observed fishing at Rib and Northwest Reefs at one time, while up to three boats were observed (anchored) at Little Kelso and Tryon Reefs at one time, and no boats were observed at Bandjin or Wreck Reefs at any time. This steep gradient of human presence is typical for these reefs and occurs year-round (J. Aumend, surveillance unit, Great Barrier Reef Marine Park Authority, pers. comm.). Thus, fished, no-take and no-entry reefs represent a steep gradient in the frequency of shark-human interactions. Estimates of abundance were recorded for whitetip reef sharks, *Triaenodon obesus,* grey reef sharks, *Carcharhinus amblyrhynchos* and blacktip reef sharks, *C. melanopterus*, as they are the dominant shark species on Indo-Pacific coral reefs (Robbins et al. 2006; Sandin et al. 2008; Ceccarelli et al. 2014). Multiple previous studies have demonstrated that the majority of all three reef shark species exhibit a high level of site fidelity, typically remaining on single reefs for long periods of time (Speed et al. 2011, 2012; Whitney et al. 2012; Vianna et al. 2013). Although reef sharks are capable of moving large distances in relatively short periods of time, only a small proportion of individuals move between reefs (Heupel et al. 2010; Field et al. 2011; Barnett et al. 2012; Whitney et al. 2012). This supports our assumption that inter-reef movements are sufficiently infrequent to establish and maintain a strong gradient in the frequency of human interactions experienced by sharks in the different management zones.

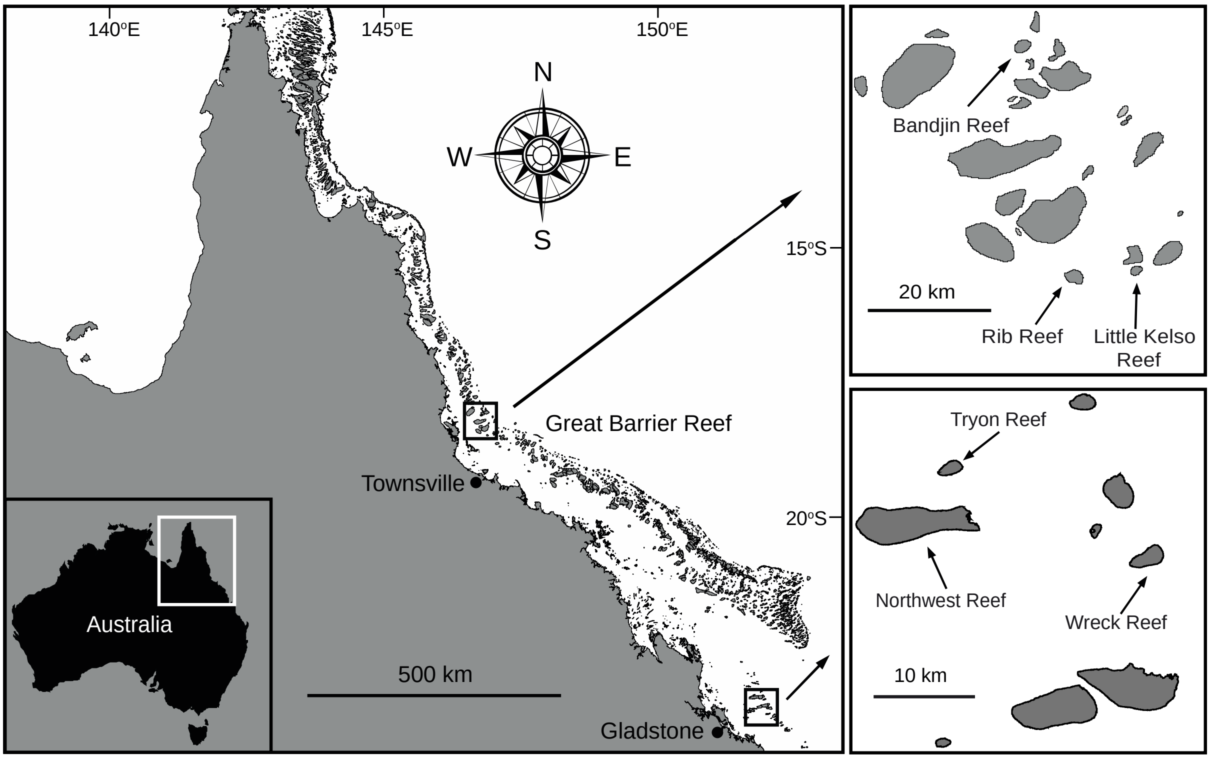

Fig. 2.1. Map showing the location of study sties. Rib and Northwest Reefs are within fished zones, Little Kelso and Tryon Reefs are within no-take zones, and Bandjin and Wreck Reefs are within no-entry zones.

Survey methodology

Survey methods consisted of timed-swims, towed-diver, SPC, ASC, BRUV (described below). Fourteen to 24 surveys were performed per method per reef, except for the towed-diver method, which entailed five to eight surveys per reef due to the large size of each replicate tow (~1.5 km) relative to the size of each reef and the need for spatial separation between replicate tows. For all survey methods, replication was stratified across three habitat types (reef slope, reef flat, back reef); however, shark counts on the reef flat were too low (<8% of total sharks observed) to allow parameter estimation in our encounter rate and generalized linear model analyses, so we focus our analysis on the slope and back reef data only. When a shark was observed, we recorded the time (to the nearest second), species, and other identifying characteristics such as estimated total length (TL), colour patterns, and scars, to minimize the risk of multiple-counting of the same individuals. In a subset of timed-swims (minimum of 10 per reef), the behavioural response of individual sharks was recorded at the moment they were first sighted (one observation per shark). Responses were categorized as ‘evasive’ (immediate change of direction away from the diver), ‘interested’ (direct, head-on approach or immediate change of direction toward the diver) or ‘neutral’ (no change of direction), as per Cubero-Pardo et al. (2011). Replicate surveys were separated by a minimum distance of 500 m, and different survey methods were performed during different weeks to avoid habituation. Each method was implemented in random order through time and space, except that Rib, Little Kelso and Bandjin Reefs were visited during November 2011-June 2012 and Northwest, Tryon and Wreck Reefs were visited during April-May 2013.

Timed-swim surveys involved a diver swimming for 45 min, which closely corresponds to that used in previous shark-specific studies (Robbins et al. 2006; Ayling and Choat 2008), but involves longer transects than those used in more taxonomically broad fish count studies (Friedlander and DeMartini 2002; DeMartini et al. 2008; Sandin et al. 2008). Towed-diver-surveys were designed to be similar to those used in other shark-specific studies (e.g. Richards et al. 2011; Nadon et al. 2012). Specifically, they involved a diver towed 60 m behind a small outboard powered vessel (6.2 m in length) for 24 min at a constant speed of approximately 1.5 knots. A distance of 60 m was chosen in order to maximize the distance between the observer and tow-vessel and limit any potential confounding effects on shark behaviour as a result of vessel noise. The observer used a small tow-board (40 cm x 60 cm), constructed of marine-grade plywood, with handholds and a secured data sheet, connected to the 60 m trailing line. For both timed-swim and towed-diver-surveys, only sharks in front of, and within 10 m either side of, the observer were counted (20 m transect width). A GPS unit (towed at the surface during timed-swims) was used to calculate survey area and enable standardization of data to units of density (ha^{-1}). The mean length (± standard error, SE) of timed-swim and towed-diver-surveys was 779 ± 22 m and 1618 ± 49 m, respectively.

Stationary-point-count (SPC) involved a diver scanning 360^o from a fixed point and counting all sharks observed within a 10 m radius during a 3 min period. Short survey duration is standard for SPC (Samoilys and Carlos, 2000) and is intended to reduce bias caused by shark behaviour (Ward-Paige et al. 2010a). This protocol differs slightly from other studies (e.g. Bohnsack and Bannerot, 1986; Nadon et al. 2012), where for vagile species, such as sharks, if multiple individuals are observed during the sampling time period, only the first individual is recorded in the quantitative data.

Audible-stationary-count (ASC) surveys were similar to SPC except that the diver rapidly and repeatedly squeezed the sides of an empty plastic drink bottle. Recreational divers know this method as the ‘squeaky-bottle’ technique because it attracts sharks via emission of low frequency sound. Each survey lasted for 10 min and commenced after a 3 min acclimation (silence) period. To convert counts to an estimate of absolute density (and thus enable comparison of ASC with other methods), it was necessary to estimate the distance over which sharks responded to the auditory stimulus (i.e. to estimate the area of attraction, AoA). Sharks have excellent hearing that enables them to rapidly localize and home-in toward low frequency sounds that are up to 250 m away (Nelson and Gruber 1963; Myrberg 2001). However, the average response distance is likely to be considerably less than

250 m because of individual variation (Myrberg 2001). By placing an acoustic transmitter at a known distance from a multi-species shark aggregation site in the Bahamas, Myrberg et al. (1976) demonstrated that a suite of shark species could be reliably attracted to low frequency sound at a distance of 80 m, with a modal response time of approximately 1 min. During a pilot study on the GBR, we found that reef sharks (*T. obesus* and *C. amblyrhynchos*) responded to 'squeaky-bottle' sounds with temporal characteristics (e.g. mean time to first arrival and modal response time) that were almost identical to those reported by Myrberg et al. (1976). Therefore, the response distance for the present study was assumed to be approximately 80 m and the theoretical AoA was estimated as:

$$\mathrm{AoA}_{\mathrm{ASC}} \approx \pi r^2 / 10^4,$$

where r is the radius (80 m) and 10^4 converts m^2 into hectares. Using this simple model, we estimated that the AoA for ASC surveys was 2.01 ha. Note that, for comparisons of ASC counts on different reefs or in different habitats, this conversion of counts to density has no effect, since all counts are converted by the same constant. Any biases in the estimate of density would influence only comparisons of abundance across methods (and are considered in the Discussion).

Baited-remote-underwater-video (BRUV) units consisted of a steel frame and centrally-mounted plastic housing which contained a battery-operated video camera (Cappo et al. 2004, 2007). A bait bag containing approximately 1 kg of crushed pilchards (*Sardinops sagax*) was mounted 1.5 m from the front of the camera, and filming occurred continuously for 60 min after deployment. Previous BRUV studies presented results as time-to-first-arrival (Priede and Merrett 1996), maximum number of individuals viewed at any one time (MaxN; Willis et al. 2000), or catch-per-unit-effort (CPUE, the number of individuals 'caught' on film; Brooks et al. 2011). In the present study, we used total catch as the preferred index of abundance because (1) soak time was uniform (60 min), (2) sharks were relatively rare, such that MaxN was consistently small and meaningless, and (3) individual sharks could be readily identified from their unique characteristics (see above), which helped to avoid double-counting.

To estimate absolute density (and thus enable comparison of BRUV with other methods), it was necessary to estimate the area over which the bait plume dispersed in 60 min (i.e. estimate the AoA). To do this, a SCUBA diver released 30 ml of red food dye underwater. After 3 min, the distance and angle of dye dispersal was calculated via tape measure and trigonometry. After ten trials at representative locations and tide cycles, mean current velocity and dispersal angle was calculated to be 3.40 m min^{-1} and 23.5^{o} respectively. These results are similar to published hydrodynamic data for the GBR (Cresswell and Greig 1978; Wolanski and Jones 1980) and correspond to observed dispersal patterns of pilchard oil under prevailing conditions (authors' pers. obs.). Accordingly, the AoA was approximately:

$$\text{AoA}_{\text{BRUV}} \approx \pi(T_{\text{soak}} \times V_{\text{current}})^2 \times A_{\text{d}} \; / \; 10^4,$$

where T_{soak} is the duration of filming (60 min), V_{current} is the water current velocity (3.40 m min^{-1}), A_{d} is the angle of dispersal (23.5^{o}; expressed as a proportion of 360^{o}), and 10^4 converts m^2 into hectares. Using this simple model, we estimated that the AoA for BRUV surveys was 0.85 ha. As with the AoA for ASC surveys, this conversion does not affect comparisons of abundances between reefs or habitats because all BRUV counts were normalized by the same constant.

Data analysis

To test for biases due to shark behavioural responses to divers, two types of analyses were performed. Firstly, a ‘scaled’ χ^2 homogeneity test (Lawal and Upton, 1984) was used to evaluate the distribution of behavioural responses (evasive, interested, neutral) during timed-swim surveys in each management zone. Secondly, we fit several alternative models for shark encounter rates. In the first model, shark encounter rate is high (or low) initially, and then asymptotically approaches a baseline level over time:

$$f_{var}(t) = \mu\,(1 - \beta e^{-\alpha t}) \qquad \text{Eq. (1)}$$

where t is time elapsed since the start of the transect, β is the bias (the amount by which the encounter rate is elevated above baseline at the start of the transect), and α is the rate at which that encounter rate asymptotically approaches the baseline (β>0, α >0 implies attraction when divers enter the water; β<0, α<0 implies avoidance). μ is a normalization constant: because $f_{var}(t)$ is a probability distribution, it must integrate to 1. μ is normalization constant (since Eq. 1 is a probability distribution, it must integrate to 1):

$$\mu = \frac{\alpha}{\alpha\, t_f - \beta\,(1 - e^{-\alpha t_{max}})} \qquad \text{Eq. (2)}$$

where t_{max} is the duration of the transect. We used maximum likelihood methods to estimate the values of α and β that provided the best fit of Eq. (1), given the observed encounter times of sharks, and the replicate duration t_{max}. We considered the following models where the parameters α and β: (1) vary between reefs and habitats, (2) are identical for reefs within the same management zone, but vary between management zones and habitats (as might be expected if sharks' attraction to divers depends upon their past experience with human interaction), (3) are the same across management zones but differ by habitat, and (4) are the same across all management zones and habitats. We also fit a model (5) assuming no bias in the counts (β=0), implying that sharks were encountered at a constant rate. We used likelihood ratio tests to assess the evidence for bias in encounter rates, and if it was present, whether the degree of bias varied among habitat, management zone, or reef.

To test for differences in abundances between zones, habitats, and survey methods, we used a generalized linear mixed model (GLMM), using the MASS library's function glmmPQL() in R (R Development Core Team 2012), with reef included as a random effect, and a quasi-poisson error structure. The choice of a quasi-poisson error structure was made because the data were count-based, and because log-log plots of mean versus variance of density (among replicates within reefs) suggested an approximately linear relationship with a slope greater than one, indicating overdispersion (Fig. 2.2). This relationship was consistent across methods, management zones, and habitats, except for stationary-point-counts (SPC), which were clearly offset from the common mean-variance relationship (diamond-shaped points at the upper right of Fig. 2.2). However, for this method, the effective survey area was extremely small, and only seven sharks were observed on 91 surveys. Thus, confidence intervals on mean density estimates for individual reefs typically ranged from <0.1 to >10 sharks per hectare, far greater than any of the other methods. This means that SPC contains virtually no meaningful information about density, and, moreover, that including this method risked biasing the estimated variance inflation factor in the quasi-poisson GLMM (due to its departure from the mean-variance scaling relationship shown in Fig. 2.2). Consequently, SPC was excluded from the GLMM analysis. Because the quasi-poisson error structure is not a true probability distribution, likelihood-based model selection (e.g. likelihood ratio tests, AIC, BIC, etc.) could not be used. Instead, we adopted a sequential testing procedure based on the *P*-values of individual effects: starting with the full model containing all fixed effects and interactions, we removed the non-significant highest-order interaction terms in sequence until all remaining terms were statistically significant. As a check on the robustness of this analysis, we removed the random effect of reef from all models, re-fitted the entire model set, and conducted model selection using a quasi-likelihood procedure based on adjusted model deviances (Zuur et al. 2009).

Different shark species tend to have slightly different behaviours: *C. amblyrhinchos* and *C. melanopterus* swim constantly and are relatively timid, whereas *T. obesus* often rest on the seafloor and are less timid (Cubero-Pardo et al. 2011). To test whether differences in species-specific behaviour affect estimates of abundance, frequency distributions of shark species among survey methods were analysed by a 'scaled' χ^2 homogeneity test (Lawal and Upton, 1984). Detection rates of all survey methods were calculated as the proportion of surveys where one or more reef sharks was observed.

2.4 Results

We found no direct observational evidence of differences in behavioural responses to divers across management zones. Individual sharks were found to be visibly unique (in terms of species, size, sex, colour patterns, scars, etc.) and no shark was knowingly observed more than once during a single survey. Frequency distributions of behavioural responses among management zones were homogeneous ($\chi^2_4 = 4.21$, $P > 0.25$; Fig. 2.3). Across all management zones, only a small proportion of sharks were evasive (6-23%) or interested (9-18%), with the majority of sharks behaving neutrally (64-78%) and showing no apparent behavioural response to the diver, regardless of taxon or management zone. Similar findings were obtained when behavioural responses were considered separately by species (Fig. 2.3).

Encounter rates of sharks did not exhibit significant differences between reefs within management zone, or between management zones, for any method for either slope or back reef habitats (Table 2.1). Indeed, consistent with our behavioural observations, we found no evidence of elevated initial rates of encounter with sharks, with the exception of ASC, where the near-instantaneous transmission of sound beyond the diver's field of vision would be expected to attract sharks rapidly. Specifically, the best-fitting probability distributions of times of observation were uniform (i.e. constant over time) for the timed-swim, towed-diver, and BRUV surveys (Fig. 2.4a-c; Table 2.2). For ASC, there was statistically significant support for initially high encounter rates that decreased over time (Fig. 2.4d; Table 2.2); however, there was no evidence for differences in the strength of this effect among management zones (Table 2.1). Model selection by AICc (not shown) yielded the same best-fitting model for each method as the likelihood ratio tests.

The analysis of abundances based on GLMMs yielded strong evidence for main effects of survey method, management zone, and habitat on shark density, but not for any two-way or three-way interactions (Fig. 2.5; Table 2.3). Specifically, towed-diver density estimates were significantly lower than those of the other three methods, but ASC, timed-swim, and BRUV were highly consistent with one another (Fig. 2.5; Table 2.4). Specifically, 95% confidence intervals on effect sizes for survey method indicate that BRUV, ASC and timed-swim surveys differ at most by no more than about ~30-45%, whereas towed-diver surveys were estimated to be approximately two- to nine-fold (200-900%) lower than the other methods. Shark densities in no-entry zones were also significantly higher than densities in fished zones. Mean densities also were higher on no-take reefs than fished reefs, but the difference was non-significant (Fig. 2.5; Table 2.3). In addition, shark abundances were significantly higher on the reef slope than the back reef (Fig. 2.5; Table 2.3). When we excluded the random effect of reef, and conducted model selection based on adjusted deviances, we obtained a slightly different best-fitting model: management zone × habitat interactions were included in the best-fitting model (the magnitude of the increase in abundance on no-entry and no-take reefs relative to fished reefs was different on the slope and the back reef). However, the effects of survey method were unchanged (BRUV, ASC and timed-swim produced comparable estimates; towed-diver estimates were significantly and substantially lower) (Fig. 2.6; Table 2.5).

All three shark species (*C. amblyrhynchos, C. melanopterus,* and *T. obesus*) were observed at each of the six reefs. However, *C. melanopterus* were observed in far fewer numbers than were either of the other two species, regardless of survey method (Table 2.6). The frequency distribution of shark species among survey methods was significantly different ($\chi^2_8 = 51.76$, $P < 0.001$). In general, timed-swim and baited-remote-underwater-video (BRUV) surveys recorded more *C. amblyrhynchos* than *T. obesus*, but towed-diver surveys recorded up to four-fold more *T. obesus* than *C. amblyrhynchos*. On average, each survey method recorded one or more sharks per replicate survey, except stationary-point-count (SPC), which detected only seven sharks in a total of 91 surveys. Except for SPC, all survey methods yielded detection rates greater than 0.50 (all species combined). Audible-stationary-count (ASC) yielded the highest detection rates for *C. amblyrhynchos* (0.42), *T. obesus* (0.45) and all species combined (0.58) (Table 2.6). There were no consistent patterns in variability (i.e. coefficient of variation) among survey methods, although variability was generally higher in the fished zone than in the no-entry zone (Table 2.7).

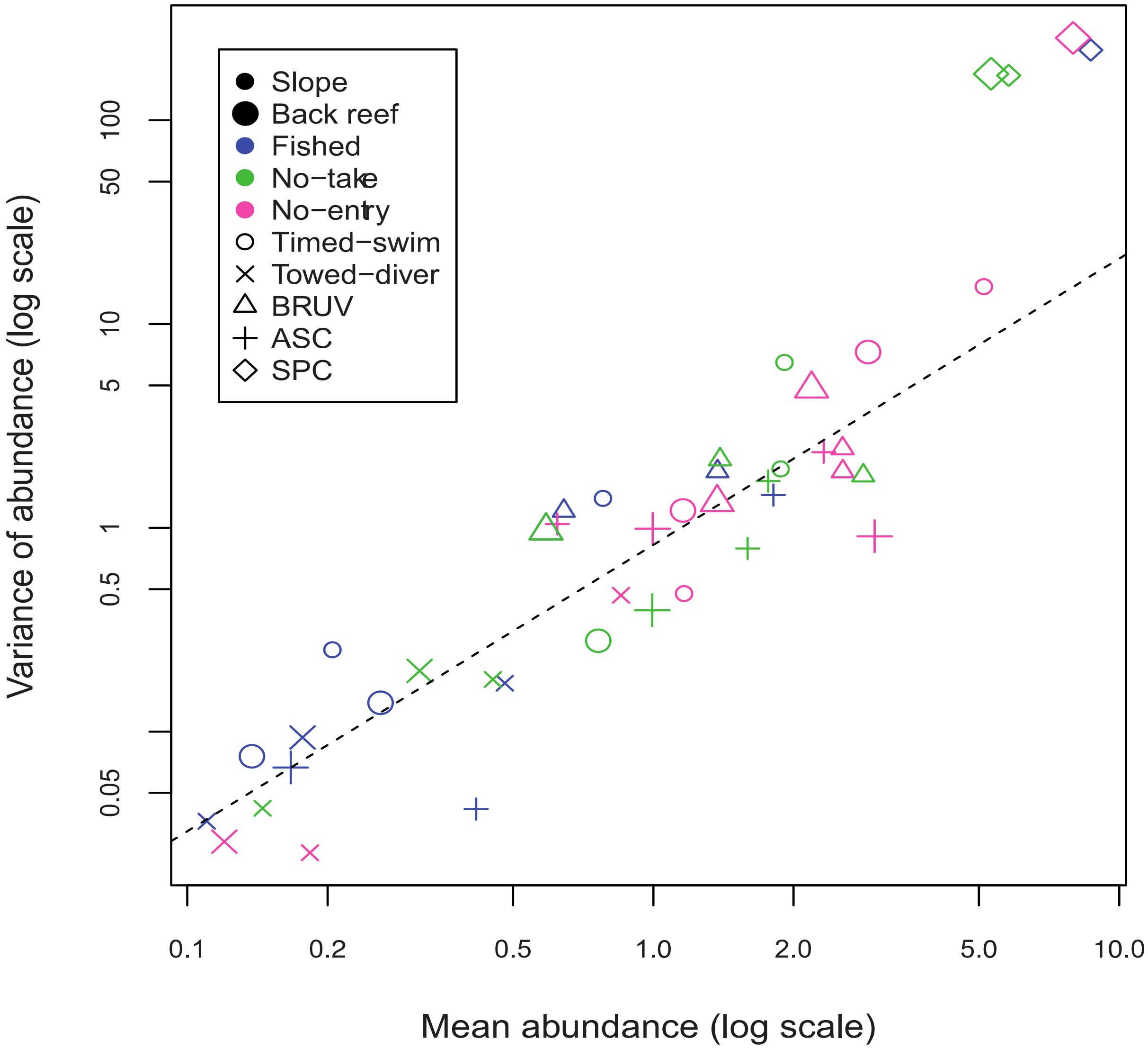

Fig. 2.2. Mean-variance scaling relationship for population density estimates. Each point shows the mean and variance among replicate surveys for each reef. Symbol sizes denote different habitats, colours denote management zones, and symbol types denote different survey methods. The regression line illustrates the common mean-variance scaling relationship for all methods except SPC (slope=*1.4*±*0.1*). Note that, because the data are plotted on a log-scale, reefs with zero observations (i.e. zero mean and variance) do not appear on the graph. Survey methods are BRUV, baited-remote-underwater-video; ASC, audible-stationary-count and SPC, stationary-point-count.

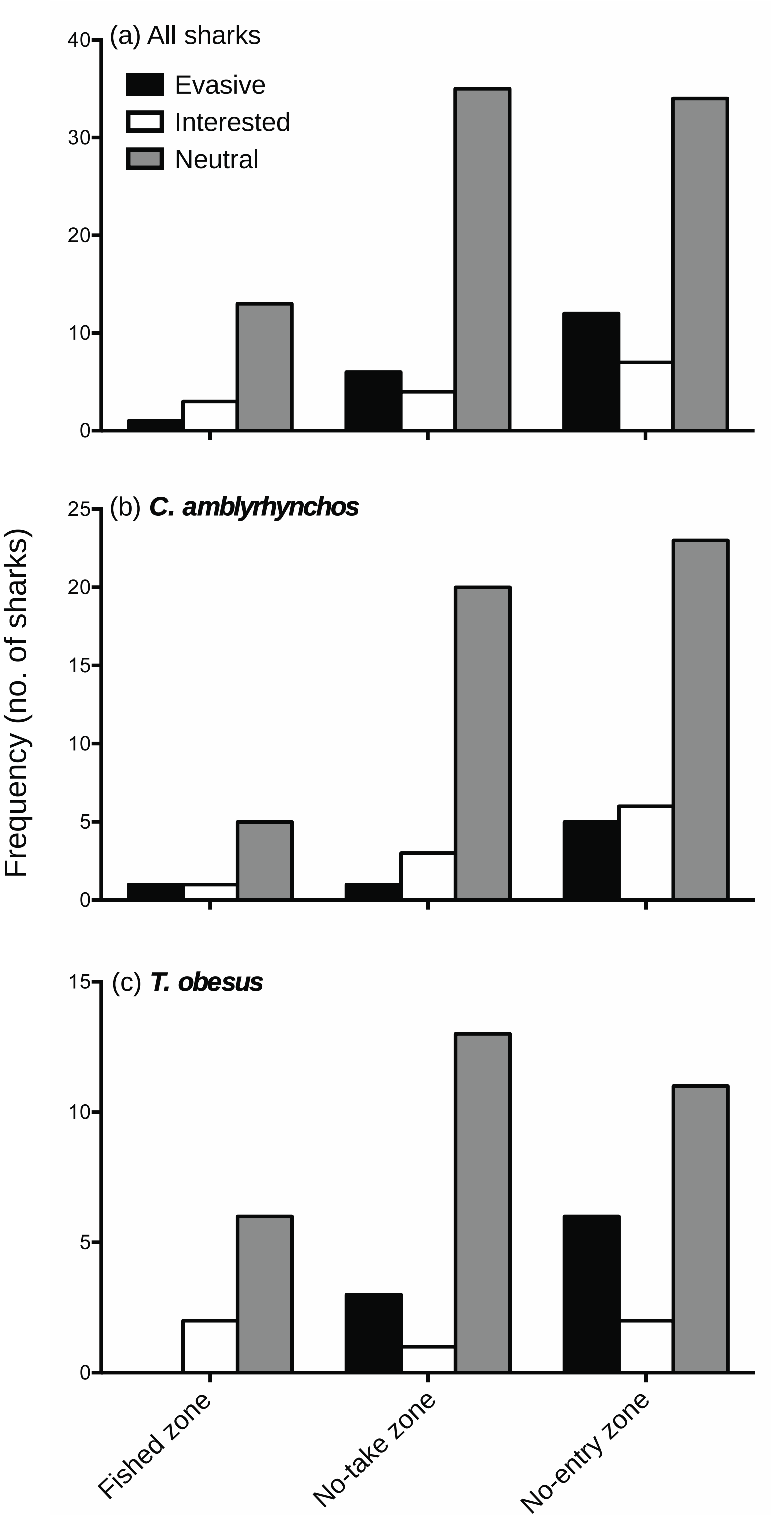

Fig. 2.3. Behavioural responses of sharks to a SCUBA diver at fished, no-take and no-entry zones. Data are presented for (a) all sharks combined (including *Carcharhinus melanopterus*), (b) *Carcharhinus amblyrhynchos* and (c) *Triaenodon obesus*. Note that *C. melanopterus* was not analysed separately as too few sharks were observed to warrant meaningful comparisons. Response categories are defined in the Materials and methods section. Note different scales of *y*-axes.

Table 2.1. Results from likelihood ratio tests for the variable-rate models of shark encounter. The effects of reef, management zone, and habitat on shark encounter rate are shown for timed-swim, towed-diver, baited-remote-underwater-video (BRUV) and audible-stationary-count (ASC) survey methods. *R* is the likelihood ratio statistic. A statistically significant result indicates rejection of the simpler model (with reef, management zone, or habitat pooled) in favour of the more complex one (with different parameters for different reefs, management zones, or habitats, respectively). For instance, the tests under "Reefs (within management zone)" show that reefs from the same management zone do not differ significantly in their encounter rate parameters (Eq. 1).

Method[a]	Reefs (within management zone)						Management zone (reefs pooled)						Habitat (management zones pooled)		
	Slope			Back reef			Slope			Back reef					
	R	df	*P*	*R*	df	*P*	*R*	df	*P*	*R*	df	*P*	*R*	df	*P*
Timed-swim	1.76	6	0.94	0.87	2	0.65	1.81	4	0.77	0.66	4	0.96	0.75	2	0.69
Towed-diver	-	-	-	-	-	-	7.31	4	0.12	-	4	-	0.97	2	0.62
BRUV	2.47	6	0.87	2.81	2	0.25	2.16	4	0.71	2.38	4	0.67	2.61	2	0.27
ASC	9.16	6	0.17	0.48	2	0.79	8.23	4	0.08	2.33	4	0.68	1.24	2	0.54

[a] '-' indicates insufficient data

Table 2.2. Results from the likelihood ratio test comparing, for each survey method, the best-fitting variable-rate model of shark encounter from Table 2.1 (management zones and habitats pooled) with a constant rate model.

Method[a]	*R*	df	*P*[b]
Timed-swim	2.32	4	0.68
Towed-diver	3.02	4	0.55
BRUV	7.66	4	0.11
ASC	31.98	4	< 0.001*

[a] Survey methods: ASC, audible-stationary-count; BRUV, baited-remote-underwater-video

[b] Statistically significant differences ($P < 0.05$) indicate rejection of the constant-rate model in favour of the variable-rate model

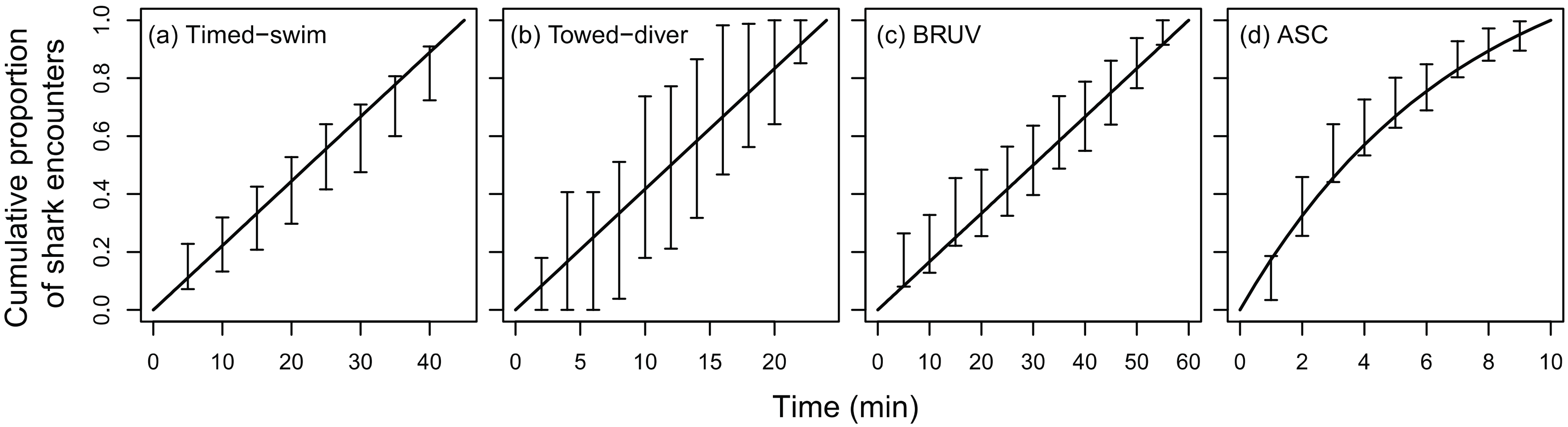

Fig. 2.4. Observed cumulative proportion of shark encounters (mean ± 95% confidence intervals) through time during (a) timed-swim, (b) towed-diver, (c) baited-remote-underwater-video (BRUV), and (d) audible-stationary-count (ASC) surveys. Best-fit cumulative distributions from the encounter rate models, as indicated by model selection, are the thick solid lines. Note that a straight diagonal line (a-c) indicates a constant encounter rate model, whereas a decelerating line (d) indicates higher encounter rates earlier in the survey. For each survey method, all samples were combined for model fitting. Note different scales of *x*-axis.

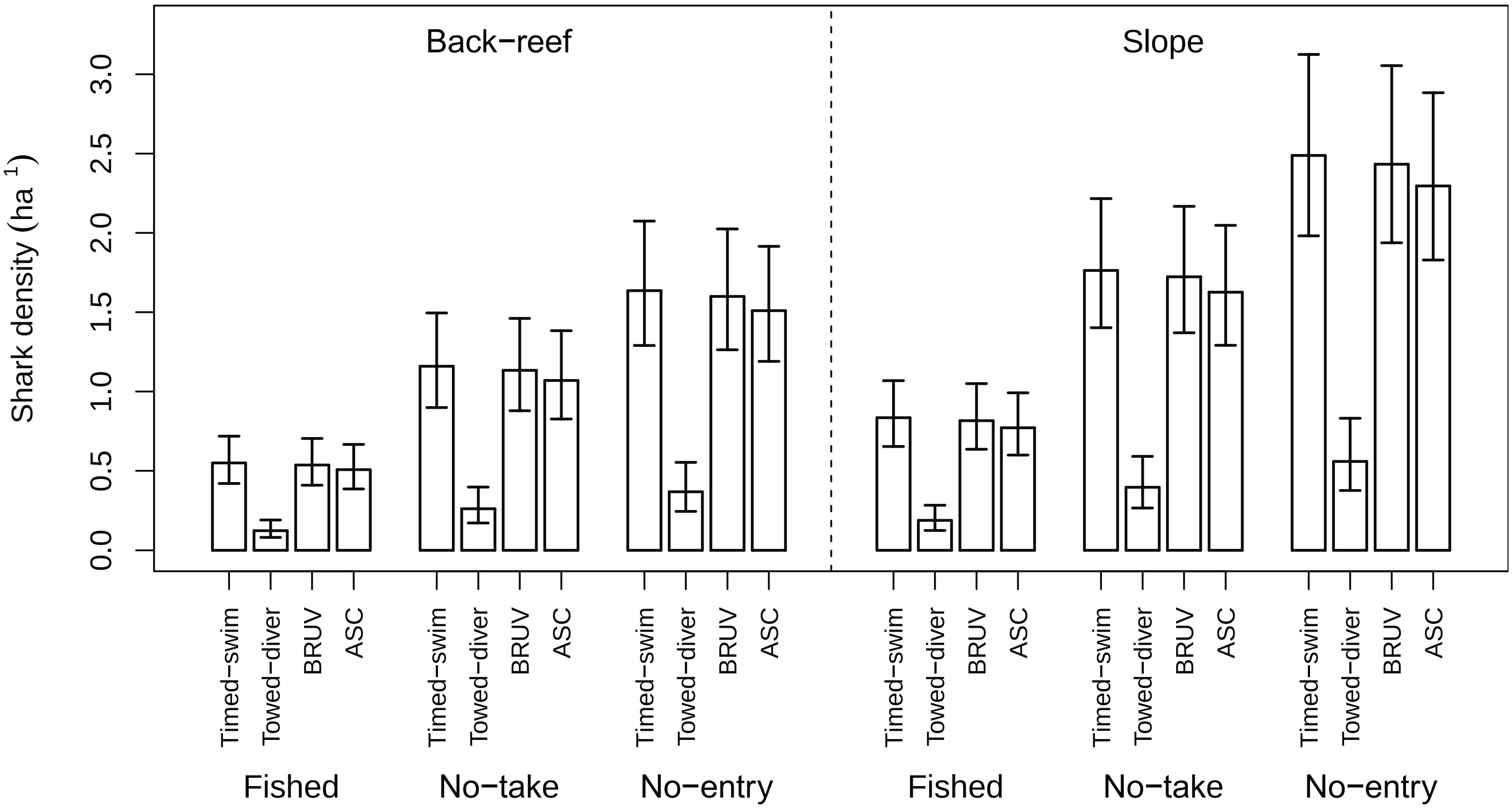

Fig. 2.5. Estimates of absolute shark density (mean ± standard error) as a function of management zone (degree of human interaction), survey method and habitat, from the fitted GLMM (Table 2.3). For baited-remote-underwater-video (BRUV) and audible-stationary-count (ASC) surveys, absolute density was estimated using an area of attraction (AoA) model (see Methods section).

Table 2.3. Parameter estimates for the best-fitting generalized linear mixed-effects (GLMM) model, with a random effect of reef, and a quasi-binomial error distribution. Note that the response variable is log-transformed. The "intercept" parameter corresponds to the predicted natural logarithm of density (ha^{-1}) for the back reef habitat in a fished zone that was surveyed by the towed-diver method. All other terms represent effect sizes. Colons indicate interactions. For example, the predicted natural logarithm of density for a timed-swim on the reef slope in a no-take zone would be Intercept + Method (Timed-swim) + Zone (No-take) + Habitat (Slope), or -2.09 +1.49+0.75+0.42 = 0.57, implying $e^{0.57}$=1.77 sharks ha^{-1}. The estimated standard deviation for the random effect of reef was 0.26 (95% CI: 0.12-0.54); the estimated residual standard error was 1.10 (95% CI: 1.00-1.20). n =246.

Effect[a]	Estimate	SE	df	*t*-statistic	*P*[b]
(Intercept)	-2.09	0.44	236	-4.80	< 0.0001*
Method (ASC)	1.41	0.37	236	3.85	0.0002*
Method (Timed-swim)	1.49	0.37	236	4.08	< 0.0001*
Method (BRUV)	1.47	0.37	236	4.01	< 0.0001*
Zone (No-take)	0.75	0.32	3	2.35	0.10
Zone (No-entry)	1.09	0.31	3	3.49	0.04*
Habitat (Slope)	0.42	0.14	236	2.90	0.004*

[a] Survey methods are ASC, audible-stationary-count; BRUV, baited-remote-underwater-video

[b] Statistically significant effects ($P < 0.05$)

Table 2.4. Estimated differences in log-abundance between survey methods. Comparisons with the towed-diver method are identical to the corresponding effects in Table 2.3. For comparisons among audible-stationary-count (ASC), timed-swim, and baited-remote-underwater-video (BRUV), the values are analogous. For instance, "ASC - Timed-swim" gives the ASC effect that would have been obtained if Timed-swim (rather than Towed-diver) had been the method incorporated in the intercept parameter of Table 3. P-values are calculated based on the corresponding t-statistics (df=236 in all cases). Because there are six pairwise comparisons, the critical P-value for a conventional Bonferroni correction is 0.008. In the final column, we report 95% confidence intervals on the ratio of abundances (the first divided by second) between the two methods, which are calculated from the effect size estimate and standard error as $e^{Estimate \pm 1.96\,SE}$.

Difference[a]	Estimate	SE	*t*-statistic	*P*[b]	Ratio (95% CI)
ASC – Towed-diver	1.41	0.37	3.85	0.0002*	1.98-8.46
Timed-swim – Towed-diver	1.49	0.37	4.08	< 0.0001*	2.14-9.16
BRUV – Towed-diver	1.47	0.37	4.01	< 0.0001*	2.11-8.98
Timed-swim – ASC	0.07	0.16	0.44	0.66	0.78-1.47
BRUV – ASC	0.05	0.16	0.31	0.76	0.77-1.44
BRUV – Timed-swim	-0.02	0.16	-0.13	0.90	0.72-1.34

[a] Survey methods are ASC, audible-stationary-count; BRUV, baited-remote-underwater-video

[b] Statistically significant effects (corrected alpha value of 0.008)

Table 2.5. Parameter estimates for the best-fitting model according to the quasi-likelihood model selection procedure shown in Fig. 2.6. Note that the response variable in this analysis is log-transformed. The "intercept" parameter corresponds to the predicted natural logarithm of density (ha^{-1}) for the back reef habitat in a fished zone that was surveyed by the towed-diver method. All other terms represent effect sizes. Colons indicate interactions. For example, the predicted natural logarithm of density for a timed swim on the reef slope in a no-take zone would be Intercept + Method (Timed-swim) + Zone (No-take) + Habitat (Slope) + [Zone (No-take):Habitat (Slope)], or -2.60+1.46+0.95+1.10-0.29 = 0.62, implying $e^{0.62}$=1.86 sharks ha^{-1}, (virtually identical to that estimated by the GLMM in the analysis: Table 2.3). The residual deviance was 323.5 on 237 degrees of freedom. n = 246.

Effect[a]	Estimate	SE	*t*-statistic	*P*[b]
(Intercept)	-2.60	0.560	-4.63	< 0.0001*
Method (ASC)	1.39	0.38	3.62	< 0.001*
Method (Timed swim)	1.46	0.38	3.81	< 0.001*
Method (BRUV)	1.44	0.38	3.76	< 0.001*
Zone (No-take)	0.95	0.54	1.77	0.08
Zone (No-entry)	1.87	0.45	4.17	< 0.0001*
Habitat(Slope)	1.10	0.46	2.40	0.02*
Zone (No-take):Habitat (Slope)	-0.29	0.57	-0.50	0.62
Zone (No-entry):Habitat(Slope)	-1.00	0.49	-2.04	0.04*

[a] Survey methods: ASC, audible-stationary-count; BRUV, baited-remote-underwater-video
[b] Statistically significant effects ($P < 0.05$)

Table 2.6. Total shark count and detection rates (in parentheses) for each survey method. Detection rate is the proportion of surveys in which one or more sharks were recorded. Data are pooled across management zones.

Survey method[a]	*Carcharhinus amblyrhynchos*	*Triaenodon obesus*	*Carcharhinus melanopterus*	All sharks
Timed-swim (n = 95)	89 (0.31)	60 (0.38)	7 (0.06)	156 (0.56)
Towed-diver (n = 39)	6 (0.10)	27 (0.44)	2 (0.05)	35 (0.51)
BRUV (n = 91)	53 (0.36)	36 (0.29)	20 (0.18)	109 (0.58)
SPC (n = 91)	2 (0.02)	5 (0.06)	0 (0)	7 (0.08)
ASC (n = 91)	98 (0.42)	97 (0.45)	6 (0.05)	201 (0.58)

[a] Survey methods are BRUV, baited-remote-underwater-video; SPC, stationary-point-count; ASC, audible-stationary-count

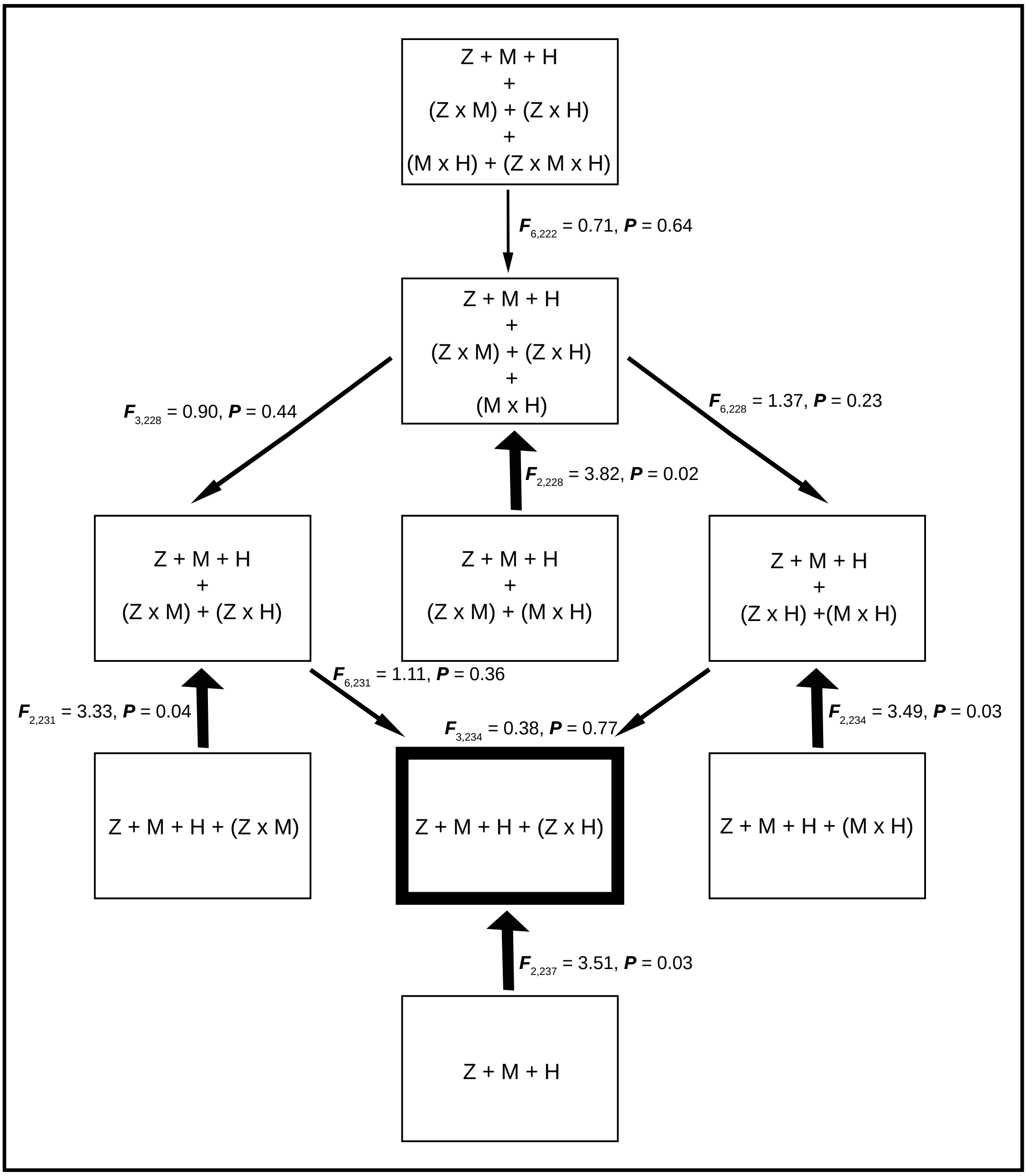

Fig. 2.6. Schematic of sequential model selection procedure for the GLM analysis, based on comparisons of adjusted model deviances using *F*-statistics (see Methods for justification). Each box is a model: Z denotes management zone, H denotes habitat, and M denotes survey method. Interactions are designated, e.g., Z × H (two-way interaction between management zone and habitat). Arrows (with corresponding *F*-statistics and *P*-values) show results of model selection. Non-significant tests (normal-font arrows pointing towards the simpler model) indicate no statistically significant support for the more complex model. Significant tests (bold arrows pointing towards the more complex model) indicate rejection of the simpler model for the more complex one. The model favored by model selection is outlined in bold.

Table 2.7. Coefficients of variation for each survey method and management zone. Data are expressed as percentages and sample sizes are shown in parentheses.

Survey method[a]	Fished zone	No-take zone	No-entry zone
Timed-swim ($n = 95$)	197	129	129
Towed-diver ($n = 39$)	137	131	129
BRUV ($n = 91$)	147	120	86
ASC ($n = 91$)	124	100	104

[a] Survey methods: BRUV, baited-remote-underwater-video; ASC, audible-stationary-count

2.5 Discussion

While there is wide agreement that reef sharks are in decline in many regions of the world, the appropriateness of baseline population estimates and the effectiveness of no-take areas for protecting shark populations have been the subject of increasing debate, especially over the past five years (Heupel et al. 2009; Hisano et al. 2011; Nadon et al. 2012). Much of the controversy has revolved around the reliability of diver-based estimates of absolute and relative abundances of sharks in areas with negligible human interaction versus areas subject to fishing. Although arguments that sharks' vagility and/or behavioural responses towards divers may bias survey outputs are plausible on biological grounds (e.g. Watson et al. 1995; Dickens et al. 2011), we find no evidence that they markedly bias abundance estimates from diver-based timed-swims, despite considering multiple lines of evidence. Firstly, behavioural responses of sharks were consistent across management zones (i.e. degree of human interaction). Secondly, shark encounter rates were not significantly higher or lower when divers first entered the water, regardless of management zone. Thirdly, estimates of shark density from timed-swims (assuming zero AoA; i.e. no attraction to divers) were comparable to densities estimated from BRUV and ASC surveys, once their respective AoA were taken into account. Fourthly, no interaction between survey method and management zone was detected for estimates of shark abundance, implying that any biases in the methods are consistent across management zones (or that biases of timed-swims, towed-diver, ASC, and

BRUV all happen to vary with management zone in exactly the same way – a possibility that seems highly implausible given the fundamental logistical differences between the methods). Finally, even the rate of decrease over time in encounter rates for ASC (specifically designed to attract sharks quickly) was not significantly different across management zones. These results suggest that estimates of shark abundance from timed-swims are robust to any attraction to or avoidance of divers by sharks.

In addition to the consistency of timed-swims with BRUV and ASC surveys in this study, timed-swim estimates of relative abundances in no-take versus fished zones are highly consistent with other studies on the GBR that have used timed-swims, and with experimental catch rate data (Fig. 2.7). Similarly, Hisano et al. (2011) found that estimated differences in abundance between no-entry and fished reefs were highly consistent with differences based on population projections using estimates of per-capita demographic rates. Our findings therefore suggest that previous conclusions drawn from shark-oriented timed-swim data are satisfactorily robust. This is important because reef sharks are vulnerable to even low levels of fishing, as might be expected in no-take areas (e.g. Davis et al. 2004; McCook et al. 2010). Hence, high abundance of sharks in no-entry zones appears to be real and not an artefact of shark behaviour towards divers, suggesting that even small no-entry zones can effectively preserve high shark abundances.

Shark density estimates were influenced by survey method, but these effects were highly consistent across management zones and habitat types. Of the four methods that we tested comprehensively, timed-swim, BRUV and ASC surveys generated consistent estimates of shark density, within ~30-45% of one another. Based on the typically low densities of sharks, most estimates show relatively high amounts of variability and broad confidence intervals. However, differences in shark densities across locations (e.g. across management zones) often span one or more orders of magnitude. As such, differences of <50% are likely to be small relative to the variation expected by chance in estimating densities for low-density, vagile species. In contrast, towed-diver-surveys generated density estimates that were substantially (~200-900%) lower than those generated by timed-swim surveys. Similarly, elsewhere in the Pacific Ocean (i.e. Hawaiian, Line and Mariana Islands), towed-diver-surveys generated density estimates that were three- to twenty-fold lower than those generated by diver-based transect surveys (which are similar to our timed-swim method: *c.f.* Friedlander and DeMartini, 2002; Sandin et al. 2008; Richards et al. 2011). Nadon et al. (2012) reconciled the differences between methods by suggesting that towed-diver-surveys reduce the positive bias of shark behaviour towards divers by rapidly moving divers into new areas to prevent aggregation effects. In the present study, however, we found no evidence of aggregation effects during timed-swims, and there was strong congruence between timed-swim and (diver-independent) BRUV surveys. Thus, in our view, it is more likely that towed-diver-surveys under-estimate shark density, perhaps due to sharks engaging in avoidance behaviour when being approached by a motorized tow-vessel.

Of the methods that we evaluated, only ASC yielded evidence of declining shark encounter rates over time. This method is designed to quickly attract sharks to a stationary point: the ‘squeaky bottle’ simulates wounded prey, to which sharks respond vigorously and can hear from approximately 80 m away (Myrberg et al. 1976; Myrberg, 2001). Audible-stationary-count (ASC) therefore enables very rapid assessment of local shark populations, which is ideal for studies that utilize catch-mark-resight methodology. The only method we trialed that was incapable of generating ecologically meaningful estimates of abundance was SPC, due to its very low survey area and consequent low shark counts (seven sharks in 91 surveys), which yielded confidence intervals spanning around three orders of magnitude of abundance. In areas with much higher shark densities, of course, SPC may produce enough sightings to provide less uncertain estimates of abundance. For instance, in a previous study at remote Palmyra Atoll, Line Islands (where reef shark density is likely much higher than on the GBR), McCauley et al. (2012) considered SPC surveys to produce acceptable abundance estimates.

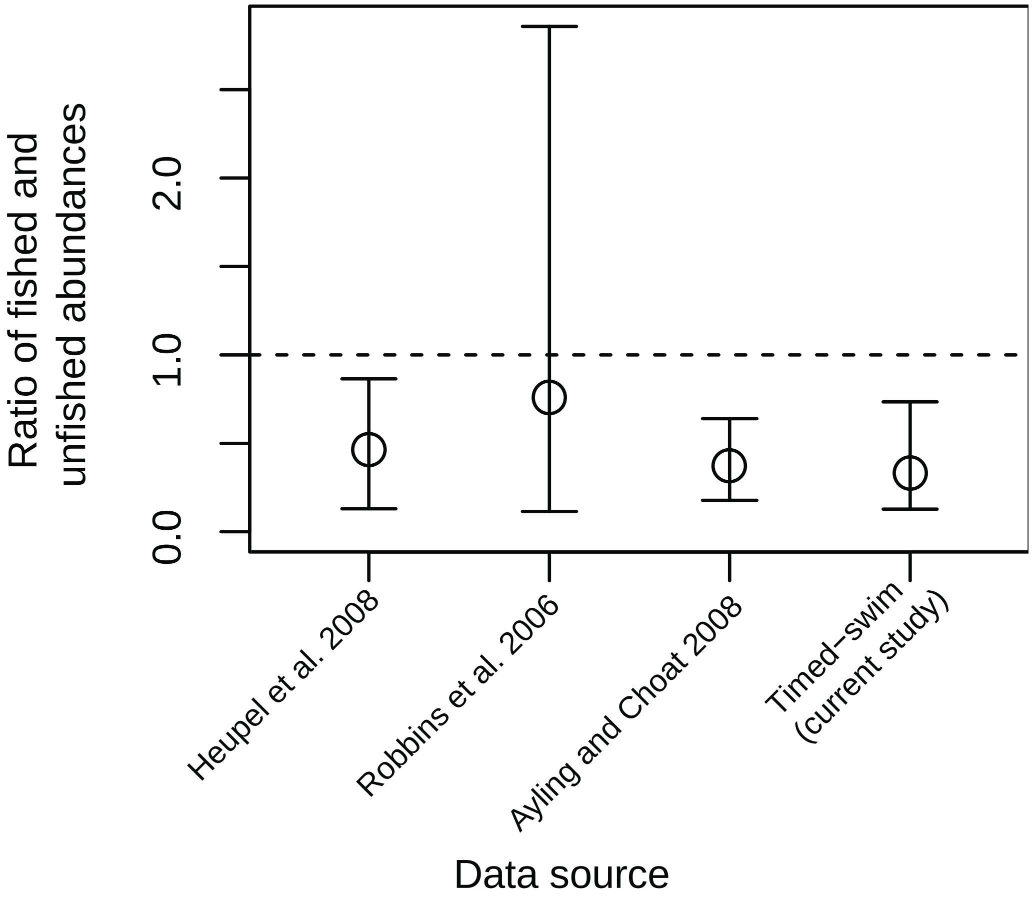

Fig. 2.7. Ratio of fished to unfished shark abundances from catch-per-unit-effort data (Heupel et al. 2008) and two other studies that used the same protocol for timed-swims as this study (Robbins et al. 2006; Ayling and Choat 2008). Whiskers indicate 95% bootstrap confidence intervals on the abundance ratios, generated by Monte-Carlo simulation (see Hisano et al. 2011). The dotted line represents where the abundance in fished and unfished zones are equal; values below the line indicate lower abundances in fished zones. Note that data are only from fished and no-take zones, as there are no catch rate data from no-entry zones. All data are from the Great Barrier Reef, Australia.

While BRUV and ASC surveys are alternatives to more conventional methods, quantitative comparisons of survey methods are challenging because it is difficult to estimate the area-of-attraction (AoA) for such surveys. In this study, we developed two models to estimate survey area and thus convert data from relative density to absolute density. However, we recognize that these first-order estimates do not account for all factors that may cause this quantity to vary. For example, results from BRUV and ASC surveys are dependent on the assumption that all species of sharks will have similar responses to attractants, such as the bait plume or sound. However, this may not be the case as there is likely to be variation in the ecology and behaviour among shark species (Bres 1994; Heuter et al. 2004). For BRUVs, the AoA will depend on a sharks' ability to detect olfactory cues associated with the bait. Further, the associated water currents will influence the dispersion strength of the bait plume. For this reason, dispersion will vary among sites and within the same site over time. For ASCs, the AoA is dependent on sound detection capabilities of different shark species. This can be severely affected by a range of biological and environmental factors (Au and Hastings 2008), which are also likely to vary over time, and according to reef topography may affect the AoA of ASC surveys. Consequently, local reef conditions may influence bait plume dispersion and sound transmission, which generates additional uncertainty regarding density estimates derived from attractant methods, such as BRUV and ASC surveys. Thus, future studies comparing locations with substantially different sound transmission properties, or small-scale circulation patterns, should assess these quantities on a site-by-site basis. Despite this, our AoA models (for BRUV and ASC surveys) generated estimates that were consistent with one another, and with the timed-swim data. In this context, it is important to note that our finding that estimates of relative abundances are comparable across survey methods (i.e. that there was no interaction between survey method and either management zone or habitat) is robust to the accuracy or otherwise of the AoA that we used, since the AoA modifies all abundance estimates for a given method by a common factor.

The fact that we found no evidence that consistent responses of sharks to divers were biasing abundance estimates, either in the timing of shark encounters or in our qualitative observations of their behavior, suggests that diver-based underwater counts can provide reliable estimates of abundance in a broad range of management situations. The extent to which our findings apply to extremely remote locations, however, depends upon the assumption that inter-reef movements of reef sharks are sufficiently infrequent that sharks in no-entry zones have little or no experience with divers. We believe that two lines of evidence support this assumption. Firstly, there have been four recent studies on movement in grey reef sharks, which are the most mobile of our study species. Three of these found high site fidelity: 85% (23 out of 27 individuals; Barnett et al. 2012), 79% (31 out of 39 individuals; Vianna et al. 2013) and 100% (26 out of 26 individuals; Field et al. 2011) of individuals remained on a single reef for extended periods of time. The exception, Heupel et al. (2010), found that 4 out of 9 tagged sharks moved between reefs. However, given that this latter study was conducted in the Ribbon Reefs of the Great Barrier Reef, a nearly contiguous reef system with very short inter-reefal distances, we believe that the balance of evidence from these studies supports relatively high site fidelity for reefs such as those we studied (for which inter-reefal distances range from about ~3-15km). Secondly, we, along with previous studies (Robbins et al. 2006; Ayling and Choat 2008), have found a large gradient in abundances of reef sharks between reefs in different management zones. This large gradient seems difficult to reconcile with very high movement rates. Nevertheless, we cannot rule out the possibility that some sharks in our no-entry reefs would have had some prior exposure to divers or boats during sojourns on reefs in other management zones.

Although no single survey method will be a panacea under all practical situations and research objectives, our findings indicate that diver-based timed-swims of the kind employed here will produce relatively unbiased estimates of absolute and relative shark abundance, comparable to those produced by diver-independent methods such as BRUV, or even auditory attraction methods used by recreational divers (ASC), once their respective AoA's are accounted for. Importantly, we find no evidence that estimated relative differences in shark abundance across gradients of human interaction vary between methods: the effect of management zone was consistent across all of the methods we considered. However, for areas that do not have very high shark densities, the low shark counts observed using the towed-diver method may reduce statistical power whenever this method is used in isolation. Previous studies using diver-based, underwater surveys have concluded that very high levels of compliance in protected areas are likely to be required to provide effective protection for species such as sharks, whose demography and life history give them very slow rates of potential population replenishment and recovery. Our findings support the robustness of the abundance estimates on which those conclusions have been based.

CHAPTER 3: Diversity, abundance, and distribution of reef sharks on outer-shelf reefs of the Great Barrier Reef, Australia

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3.1 Synopsis

Quantifying the distribution and habitat use of sharks is critical for understanding their ecological role and for establishing appropriate conservation and management regimes. On coral reefs, particularly the Great Barrier Reef (GBR), little is known regarding the distribution of sharks across major reef habitat types. In this study, we surveyed shark populations across outer-shelf reefs of the GBR in order to determine the diversity, abundance, and distribution of reef sharks across three major coral reef habitats: (1) the reef slope, (2) the back reef and (3) the reef flat. Model selection revealed that habitat was the principal factor influencing shark distribution and abundance. Specifically, overall shark abundance and diversity were significantly higher on the reef slope (and to a lesser degree, the back reef) than the reef flat. This confirms that shark populations are not homogeneously distributed across coral reefs. Thus, the results presented herein have important implications for shark population assessments. In addition, our results highlight the potential importance of the reef slope, with high levels of live coral cover and structural complexity, for sustaining reef shark populations. As this habitat is highly susceptible to disturbance events, this study provides a useful context for predicting and understanding how environmental degradation may influence reef shark populations in the future.

3.2 Introduction

Basic knowledge of habitat use is essential in clarifying the ecological role of a particular species, and for improving site-based protection approaches for species that are susceptible to overfishing and habitat degradation. Within some ecosystems, various species can influence overall habitat health. On coral reefs, for example, herbivorous reef fishes can mediate the competition for space between corals and algae, which has flow-on effects for reef diversity, productivity and resilience (e.g. Hughes et al. 2007b). Accordingly, detailed knowledge of a species abundance, distribution and habitat use is necessary to understand ecosystem links and feedbacks, thus guiding appropriate management regimes that aim to identify important areas or ecosystem functions for conservation.

Coral reefs are ecologically complex ecosystems that are in global decline due to human-induced disturbances (Pandolfi et al. 2003; De'Ath et al. 2013). Therefore, there is an urgent need to improve management of local and regional anthropogenic pressures such as fishing and habitat degradation in order to enhance reef resilience and to offset the effects of increasing global pressures such as climate change (Hughes et al. 2010). The role of large predators, particularly reef sharks, in maintaining reef resilience is unclear, but is potentially very important (Ruppert et al. 2013). At present, our understanding of the ecological role and importance of large predators on coral reefs is limited (but see Frisch et al. 2014) compared to other groups such as herbivores. Outputs of both theoretical modeling and empirical investigations indicate that reef sharks could play a major (Bascompte et al. 2005; Ruppert et al. 2013) or minor (Stevens et al. 2000; Rizzari et al. 2015) role in trophic structuring of coral reefs. Thus, widespread declines in reef shark populations (Robbins et al. 2006; Heupel et al. 2009; Nadon et al. 2012) are of great concern to coral reef mangers. Though little empirical evidence exists about the function of sharks on coral reefs, several studies have suggested correlations between shark density and benthic community structure (e.g. algae and coral cover; Sandin et al. 2008), populations of fishes at lower trophic levels (e.g. Ruppert et al. 2013) and disease prevalence and pest resistance (e.g. Dulvy et al. 2004). Furthermore, reef sharks can also modify the foraging behaviour of herbivores on a localized scale, which could have flow-on effects on the biomass and distribution of macroalgae, and the overall functioning of coral reef ecosystems (e.g. Rizzari et al. 2014b). Combined, these findings suggest that sharks may play an important role in ecosystem function (Ceccarelli et al. 2014). As such, identifying the ecological role of sharks on coral reefs is imperative for guiding management actions that aim to preserve or enhance ecosystem resilience. An important step in this direction is to quantify the distribution and habitat use of sharks on coral reefs (Papastamatiou et al. 2009a).

Habitat loss through anthropogenic activities is a major cause of global decreases in biodiversity, and shark species strongly associated with coral reefs may be more vulnerable to variations in habitat quality than those with broader habitat distributions (Wetherbee et al. 1997; Stevens et al. 2005; Garla et al. 2006; Espinoza et al. 2014). Site fidelity, or the propensity to use a particular habitat, has been observed for numerous shark species associated with coral reefs. For example, strong site fidelity has been observed in Caribbean reef sharks, *Carcharhinus perezi* (e.g. Garla et al. 2006), lemon sharks, *Negaprion brevirostris* (e.g. Murchie et al. 2010), blacktip reef sharks, *C. melanopterus* (e.g. Mourier and Planes 2013), whitetip reef sharks, *Trianeodon obesus* (e.g. Barnett et al. 2012) and grey reef sharks, *C. amblyrhynchos* (e.g. Field et al. 2011). Strong site fidelity is believed to be related to environmental factors such as prey availability or reproductive events such as mating and parturition (Powter and Gladstone 2009; Speed et al. 2010; Mourier and Planes 2013), and the degree of site fidelity (and/or habitat use) may change with ontogeny (Chin et al. 2013). When coral reefs are degraded, live corals and their associated skeletons are eroded, which can result in substantial declines in structural complexity. This may have important ramifications for reef shark populations because habitat quality can influence predator-prey interactions (Hixon and Beets 1993; Syms and Jones 2000), competition and recruitment (Carraro and Gladstone 2006). Previous research has also demonstrated that structural complexity is positively related to reef fish abundance (McCormick 1994; Gratwicke and Speight 2005) Additionally, a recent study highlighted the potential importance of live coral cover to reef-associated shark species (Espinoza et al. 2014). Therefore, understanding habitat use patterns of reef sharks is critical if we want to predict the effects of disturbance events and for establishing appropriate protocols for the conservation and management of shark populations (Simpfendorfer and Heupel 2012).

In the Indo-Pacific region, three species of sharks are highly associated with coral reef ecosystems: grey reef sharks, *C. amblyrhynchos*, blacktip reef sharks, *C. melanopterus*, and whitetip reef sharks, *T. obesus* (Sandin et al. 2008; Nadon et al. 2012; Ceccarelli et al. 2014). On the Great Barrier Reef (GBR), Australia, reef shark populations have been reported to be alarmingly low in areas subject to fishing (Robbins et al. 2006; Ayling and Choat 2008; Hisano et al. 2011). However, these reports were based on surveys that were performed on the seaward reef slope, but no surveys were conducted on other reef habitats, such as the back reef or reef flat. Sharks often have complex movement patterns within coral reef ecosystems, which makes it difficult to interpret their habitat use (Pikitch et al. 2005; Heupel et al. 2009; Heupel et al. 2010; Chin et al. 2012). Recent tracking studies using acoustic telemetry have provided insight into general habitat use patterns of reef sharks, with most shark detections occurring adjacent to the reef slope (e.g. Field et al. 2011; Barnett et al. 2012; Heupel and Simpfendorder 2014). However, fine-scale patterns in reef shark distributions across major reef habitats are poorly understood (see Dale et al. 2011 for exception). Therefore, this study aimed to characterize the diversity and distribution of reef sharks on outer-shelf reefs of the GBR, which by world standards, has a relatively intact shark community. Specifically, our objectives were (1) to compare the relative abundance and distribution of reef sharks across three major coral reef habitat types (i.e. reef slope, back reef, reef flat), and (2) determine species diversity across these habitats.

3.3 Methods

Study sites and species

This study was undertaken at three latitudinally distinct regions within the Great Barrier Reef Marine Park (GBRMP), Australia: (1) north, (2) central and (3) south (Fig. 3.1). To examine the influence of habitat association on reef shark abundance and species diversity, three replicate reefs were surveyed within each region, with the exception of the northern region, where six reefs were surveyed (Fig. 3.1). All reefs have a well-defined reef slope, back reef and reef flat, and each reef has an intact faunal community that is typical of reefs in the GBR (Newman et al. 1997; Frisch et al. 2014). Estimates of abundance were predominately aimed at whitetip reef sharks, *Triaenodon obesus*, grey reef sharks, *Carcharhinus amblyrhynchos*, and blacktip reef sharks, *C. melanopterus*, as these three species are the dominant shark species on Indo-Pacific coral reefs (Robbins et al. 2006; Sandin et al. 2008; Ceccarelli et al. 2014). However, other shark species were also recorded to assess species diversity across reef habitat types.

Data collection

Sharks were surveyed on SCUBA using 45-min timed-swims. All surveys were conducted during daylight hours and with a minimum visibility of 10 m. In this approach, a diver maintained a slow but steady swimming speed (approximately 11 m min^{-1}), whilst following the depth contour of the reef. Only sharks ahead of, and within 10 m either side of, the observer were counted (20 m transect width). A GPS unit was towed at the surface to calculate survey area and enable standardization of data to units of density (ha^{-1}). The mean survey length (± standard error, SE) was 719 ± 15 m. Sampling locations were stratified by three habitat types, 1) reef slope, 2) back reef and 3) reef flat, according to the availability of each habitat at each reef. In general, the reef slope had a steep profile and was located at the windward side of each reef. The back reef was characterized by large coral outcrops ('bommies') and/or spur-and-groove morphology and was located on the leeward side of each reef. The reef flat was typically shallow, highly planar and located between the reef slope and back reef. For a thorough description of these habitat types, see Hopley (2008). The range of replicate surveys conducted at the reef slope, back reef and reef flat was between 5-16, 3-7 and 3-4, respectively (see Table 3.1 for more details). Reduced replication in some habitats was necessary at some reefs because of the large size of each survey relative to the availability of each habitat and the need for spatial separation of adjacent transects to ensure independence. Surveys were conducted during daylight hours (0630-1800) between October-April (austral summer; to minimize seasonal variations) over three years (2011-2013; Table 3.1), and were separated by a minimum distance of 500 m. Surveys were conducted throughout the day and each habitat was sampled at different times randomly over multiple days throughout the tidal cycle. Thus, any influence of tide cycles would have been consistent across the sampling regime. During each survey, the observer swam 1-5 m above the benthos whilst continually searching above and below for sharks. When a shark was observed, the time and identifying characteristics such as visually estimated total length (TL), colour patterns and scars were recorded to minimize the risk of resurveying individuals that left and subsequently re-entered the transect area. This method is demonstrably robust for estimating shark abundance on the GBR, and has limited biases as a result of shark behaviour towards divers (Rizzari et al. 2014b).

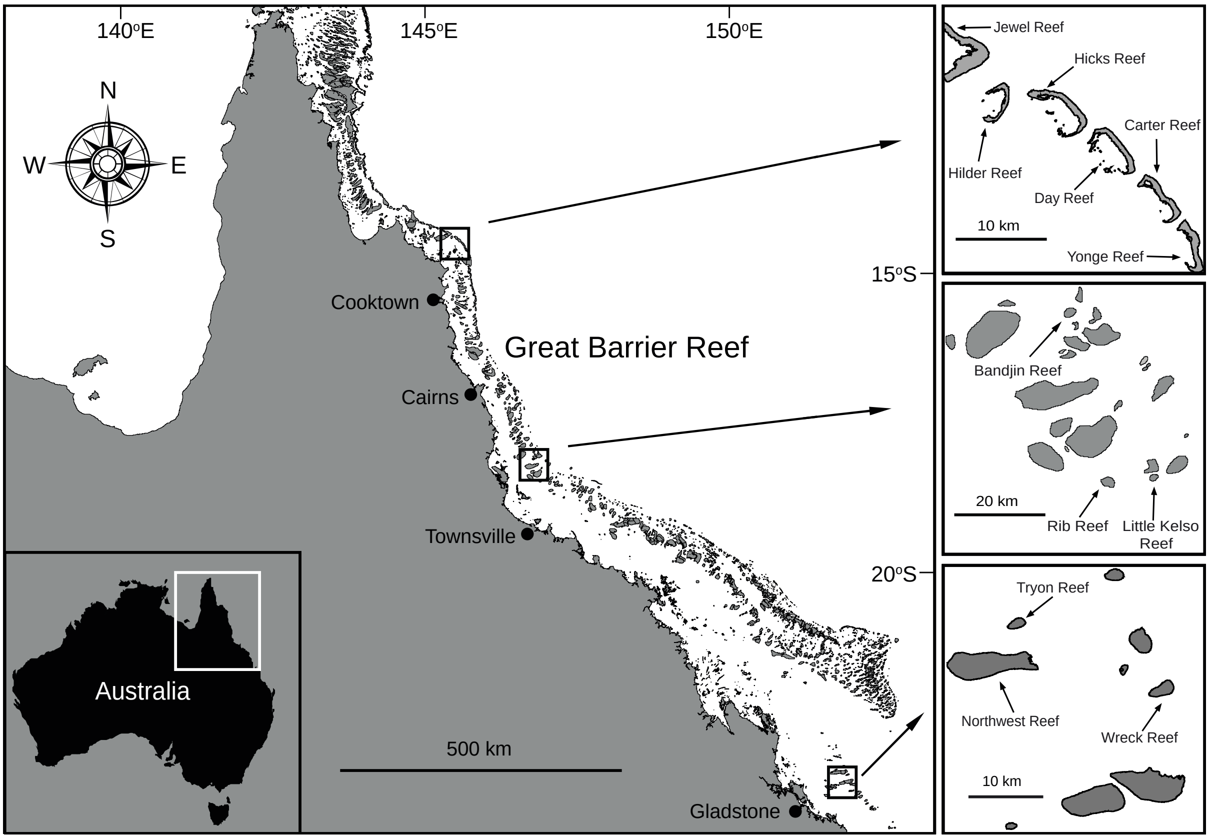

Fig. 3.1. Map showing the location of study reefs across the northern, central and southern Great Barrier Reef, Australia

Table 3.1. Summary of each reef surveyed and the associated sampling effort across the three habitat types

Region	Reef	Management zone	Reef slope	Back reef	Reef flat	Season/year surveyed
North	Jewel	Fished	6	3	4	Summer/2013
	Hilder	No-entry	6	3	3	Summer/2013
	Hicks	Fished	6	7	3	Summer/2013
	Day	No-take	6	3	4	Summer/2013
	Carter	No-entry	6	3	3	Summer/2013
	Yonge	No-take	6	3	3	Summer/2013
Central	Bandjin	No-entry	5	7	3	Summer/2012
	Rib	Fished	16	4	4	Summer/2011
	Little Kelso	No-take	8	2	4	Summer/2011
South	Tryon	No-take	7	4	3	Summer/2013
	Northwest	Fished	6	5	3	Summer/2013
	Wreck	No-entry	6	5	3	Summer/2013

To investigate habitat quality on shark community structure, live coral cover (%) and structural complexity were visually estimated in 10 m^2 areas at 5-minute intervals during timed-swim surveys. Structural complexity was categorized on a scale of one to five (based broadly on methods outlined in Wilson et al. 2007): 1) flat and sandy; 2) dominated by rubble, small rocks, algae and encrusting corals, but highly planar with few refuges; 3) abundant rocks and/or coral with limited three-dimensional structure, but occasional overhangs; 4) well developed coral or rock structures with small overhangs, but few large bommies and caves; 5) multi-layered coral matrix with caves, large bommies and abundant overhangs.

Data analysis

Variation in shark abundance and diversity were analysed using generalised linear mixed-effects models (GLMMs), with a negative-binomial error distribution to account for overdispersion and a log-link function (Zuur et al. 2009). Region, habitat, live coral cover and structural complexity were treated as fixed effects, while replicate reefs were treated as a random factor. Model selection for GLMMs was based on minimization of Akaike Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002). The top three models based on AICc values are presented, detailing changes in AICc with respect to the top ranked model (ΔAICc), AICc and model weights (wAICc). Coral cover and structural complexity across the three habitat types were compared using separate one-way analysis of variance (ANOVA) followed by Tukey's HSD test to identify significantly different groups. For each ANOVA, the relevant assumptions were checked using probability plots (for normality) and Levene's test (for homogeneity of variance). Subsequently, percent coral cover was arcsine transformed to satisfy these assumptions. A canonical discriminant analysis (CDA) was used to display variation in the structure of reef shark distribution across the three major habitat types. This analysis was based on the mean relative shark density (ha^{-1}) at each habitat within each replicate reef. All analyses were performed using the software R and the packages *glmmADMB*, *MuMIn*, and *candisc* (R Development Core Team 2013). Significant differences were considered to exist if $P < 0.05$, and all data in the text and figures are presented as the arithmetic mean ± standard error (SE) unless otherwise stated.

3.4 Results

In total, 275 individual sharks were sighted encompassing five species across the three major reef habitats (Table 3.2). The two most abundant species (*C. amblyrhynchos* and *T. obeusus*) were analysed separately in addition to the grouping of 'All sharks'. The other three species, *C. melanopterus*, *Nebrius ferrugineus* and *C. albimarginatus*, were analysed only in the grouping of 'All sharks' as their numbers were too low to provide meaningful comparisons in GLMMs (Table 3.2). Generalised linear mixed models (GLMM) indicated that, for all taxa, shark density was significantly influenced by habitat type, but not by any of the other variables included in the optimal models (Table 3.3); shark density was significantly (six-fold) higher on the reef slope than the back reef and reef flat, and significantly higher on the back reef than the reef flat, for all sharks (Fig. 3.2a) and *C. amblyrhynchos* (Fig. 3.2b). Density estimates of *T. obesus* were similar for the reef slope and back reef, however both estimates were significantly higher than density estimates on the reef flat (Fig. 3.2c). This pattern was consistent across regions (Fig. 3.3), although a high AICw suggests that region could be an important predictor of *T. obesus* density, this relationship was not statistically significant (Table 3.3). However, *T. obesus* densities were higher in the northern region compared to the central or southern regions (Fig. 3.3). Model selection also revealed that habitat was the principal driver of species richness (Table 3.4). Species richness was significantly higher on the reef slope and back reef than the reef flat; with a twofold difference in species richness between the reef slope and reef flat (Table 3.4, Fig. 3.4). Differences in both coral cover ($F_{2,\,170} = 12.66$, $P < 0.001$) and structural complexity ($F_{2,\,170} = 10.87$, $P < 0.001$) were statistically significant across the three habitat types. Specifically, both coral cover and structural complexity were significantly greater on the reef slope and back reef compared to the reef flat (Fig. 3.5). The CDA ordination plot of group centroids for each habitat displayed significant variation in reef shark species distribution (Fig. 3.6). The reef slope was predominately characterized by *C. amblyrhynchos*, while *T. obesus* was distributed across both the reef slope and back reef and *C. melanopterus* and *N. ferrugineus* with the reef flat (Fig. 3.6).

Table 3.2. Summary of total shark sightings and density (ha^{-1} ± SE) across three major reef habitat types

Habitat	*Carcharhinus amblyrhynchos* (*n* = 139)	*Triaenodon obesus* (*n* = 116)	*Carcharhinus melanopterus* (*n* = 10*)*	*Nebrius ferrugineus* (*n* = 9)	*Carcharhinus albimarginatus* (*n* = 1)	Total sharks (*n* = 275)
Reef slope	115 (1.28 ± 0.0.19)	72 (0.81 ± 0.12	2 (0.02 ± 0.01)	2 (0.02 ± 0.01)	1 (0.02 ± 0.02)	192 (2.14 ± 0.27
Back reef	24 (0.49 ± 0.18)	36 (0.85 ± 0.14)	3 (0.04 ± 0.02)	1 (0.04 ± 0.04)	0	64 (1.42 ± 0.23)
Reef flat	0	8 (0.14 ± 0.05)	5 (0.08 ± 0.05)	6 0.08 ± 0.08)	0	19 (0.31 ± 0.11

Table 3.3. Summary of optimal generalised linear mixed models (GLMM), using a negative binomial error distribution, for predicting shark density. Separate models are shown for all sharks combined, *Carcharhinus amblyrhynchos* and *Triaenodon obesus.* All sharks combined consists of *C. amblyrhynchos*, *T. obesus*, *C. melanopterus*, *Nebrius ferrugineus* and *C. albimarginatus*). Models presented are those with lowest values of the Akaike Information Criterion corrected for small sample sizes (AICc) from GLMMs that evaluate the influence of region, habitat, structural complexity and coral cover. Significant predictors are in **bold** (α = 0.05). df: degrees of freedom, ΔAICc: change in AICc with respect to the top ranked model, wAICc: AICc weights

Model	df	logLik	AICc	ΔAICc	wAICc
All sharks					
Habitat	5	-261.62	533.60	0.00	0.38
Habitat + Coral cover	6	-261.37	535.26	1.66	0.17
Habitat + Region	7	-260.46	535.59	1.99	0.14
Carcharhinus amblyrhynchos					
Habitat	5	-164.14	338.60	0.00	0.40
Habitat + Complexity	6	-163.82	340.11	1.51	0.19
Habitat + Coral cover	6	-164.05	340.56	1.96	0.15
Triaenodon obesus					
Habitat + Region	7	-171.35	357.40	0.00	0.50
Habitat + Region + Complexity	8	-171.24	359.39	1.99	0.19
Habitat + Region + Coral cover	8	-171.34	359.58	2.18	0.17

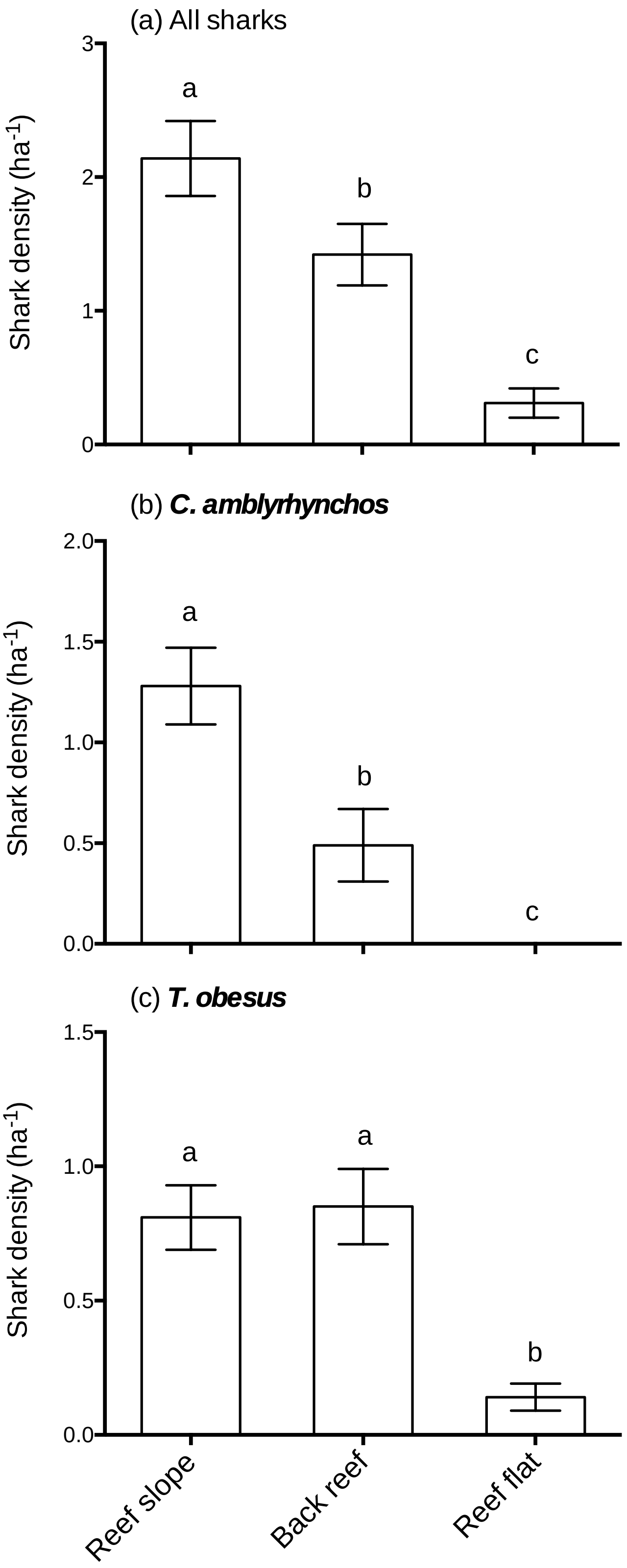

Fig. 3.2. Estimates of shark density (mean ± SE) across three major coral reef habitat types for (a) all sharks combined (b) *Carcharhinus amblyrhynchos* and (c) *Triaenodon obesus*. Note that *C. amblyrhynchos* and *T. obesus* are included in 'All sharks' along with *C. albimarginatus*, *N. ferrugineus* and *C. melanopterus*. *Carcharhinus amblyrhynchos* was never observed on the reef flat. Groups with the same letter are not significantly different.

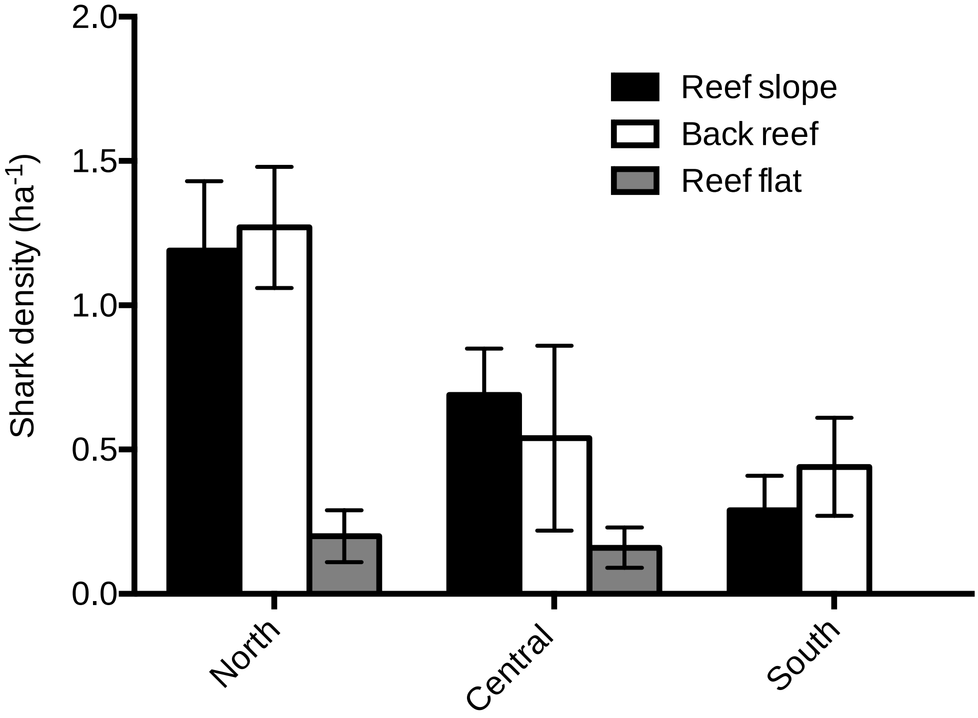

Fig. 3.3. Estimates of *Triaenodon obesus* density (mean ± SE) across three major coral reef habitats and geographic regions of the Great Barrier Reef Marine Park (GBRMP).

Table 3.4. Summary of optimal generalised linear mixed models (GLMM), using a negative binomial error distribution, for predicting shark diversity. Models presented are those with lowest values of the Akaike Information Criterion corrected for small sample sizes (AICc) from GLMMs that evaluate the influence of region, habitat, structural complexity and coral cover. Significant predictors are in **bold** ($\alpha = 0.05$). df: degrees of freedom, ΔAICc: change in AICc with respect to the top ranked model, wAICc: AICc weights.

Model	df	logLik	AICc	ΔAICc	wAICc
Habitat	**5**	-186.91	384.20	0.00	0.68
Habitat + Complexity	6	-186.89	386.31	2.11	0.24
Habitat + Complexity + Coral cover	7	-186.82	388.35	4.15	0.09

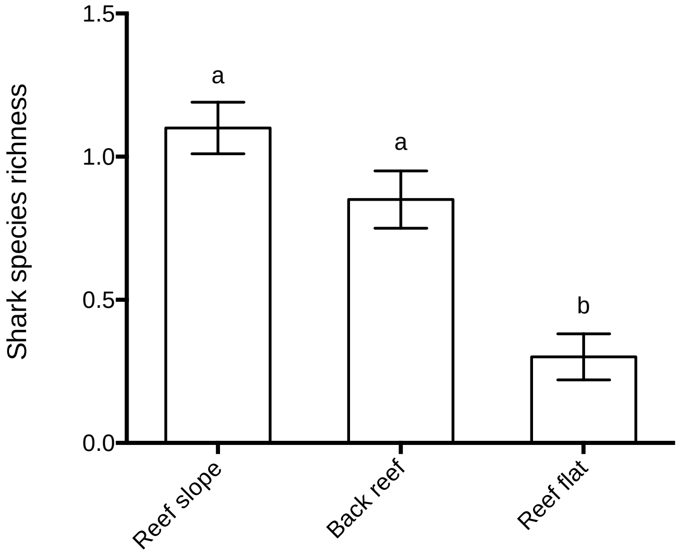

Fig. 3.4. Estimates of shark species richness (mean ± SE) across three major coral reef habitat types. Groups with the same letter are not significantly different.

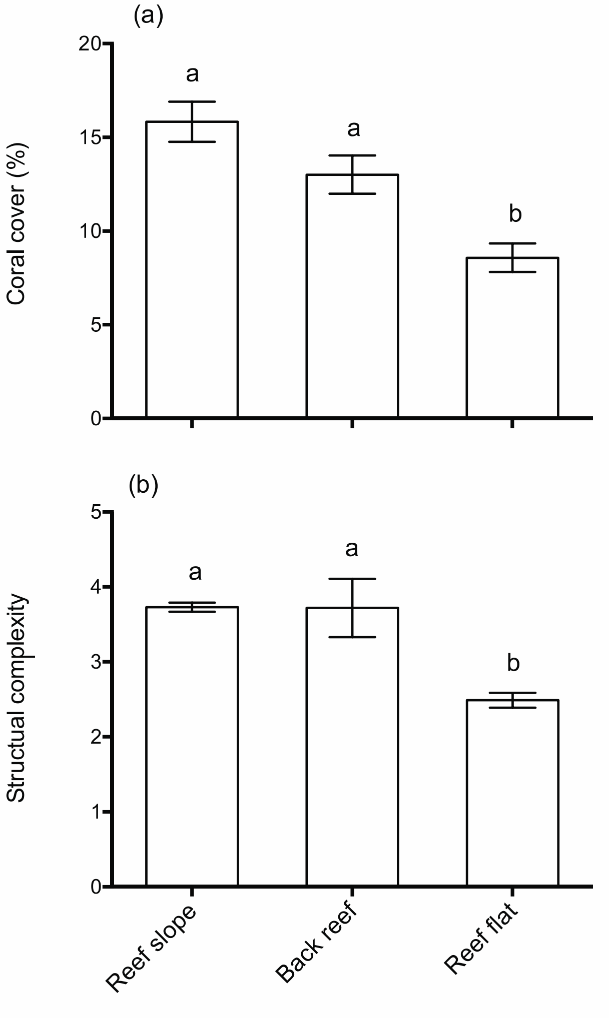

Fig. 3.5. Indices of benthic habitat quality at each habitat. (a) Percent coral cover (mean ± SE) and (b) structural complexity (mean ± SE). Structural complexity is defined in the Materials and Methods section. Groups with the same letter are not significantly different.

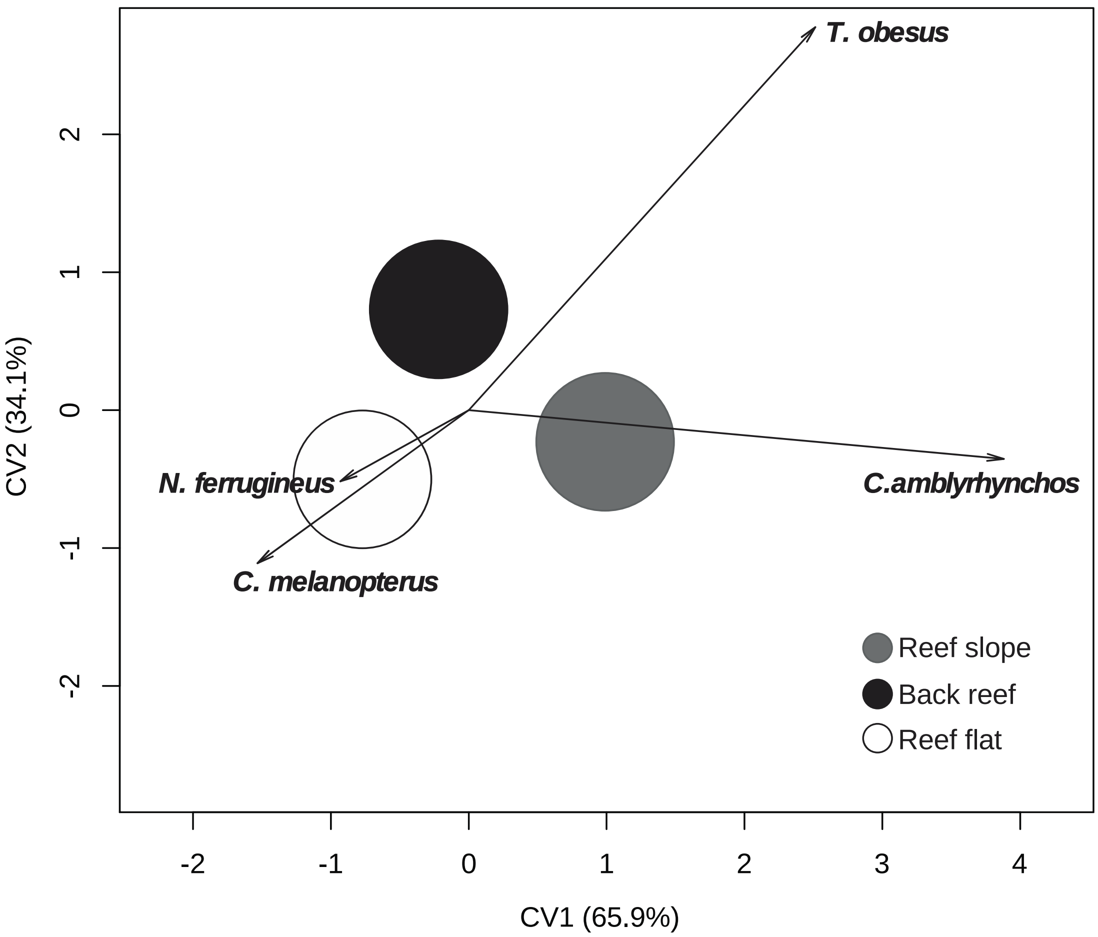

Fig. 3.6. Canonical discriminant analysis of shark species distribution across major coral reef habitats. Circles represent 95% confidence ellipses around the centroids for each habitat. Vectors represent the direction and intensity of each species' distribution across the reef.

3.5 Discussion

Understanding an organism's distribution and habitat use is imperative if we are to accurately understand their functional role and ecological impact in coral reef systems. Although numerous studies have determined the broadscale distribution of sharks on coral reefs (e.g. Hobson 1963; Randall 1977; McKibben and Nelson 1986; Robbins et al. 2006; Papastamatiou et al. 2009b) as well as general movement patterns (e.g. Heupel et al. 2010; Speed et al. 2010, 2011; Barnett et al. 2012; Vianna et al. 2013), information regarding their specific habitat distributions is lacking (but see Dale et al. 2011), particularly for the GBR.

Here, we show that, overall, reef sharks were typically six times more abundant on the reef slope compared to reef flat. This result is consistent with a previous study conducted at French Frigate atoll in Hawaii that found sharks were significantly less abundant in reef lagoons (Dale et al. 2011). *Carcharhinus amblyrhynchos* was not observed on reef flats, and density estimates for this species were higher on the reef slope compared to the back reef. This result is comparable with previous research, which observed *C. amblyrhynchos* in greater numbers on outer reef slopes that are associated with strong currents (McKibben and Nelson 1986; Wetherbee et al. 1997; Papastamatiou et al. 2006; Field et al. 2011). Furthermore, our results indicate that *T. obesus* occupies a wide range of habitats (i.e. individuals were observed at all three habitats but in greater numbers on the reef slope and back reef compared to the reef flat). Observations of the remaining three species (*C. melanopterus*, *N. ferrugineus* and *C. albimarginatus*) were limited and somewhat sporadic, thus our results regarding these species should be interpreted with a degree of caution. C*archarhinus melanopterus* was observed at all three habitats, although most frequently observed on the reef flat. This species is believed to favour reef flats and shallow lagoons and can also be found in mangrove and inshore coastal habitats (Stevens 1984; Papastamatiou et al. 2009b; Chin et al. 2013). The majority of *N. ferrugineus* observed were juveniles on the reef flat, which is consistent with previous observations of juveniles occupying crevices of shallow lagoons (Morrissey an Gruber 1993). Only a single *C. albimarginatus* was observed, which was on the reef slope, suggesting that this species may not be a reef specialist (Stevens, 1984) or that this species is difficult to count using underwater visual census (UVC) methods. Given the significantly higher density of sharks on the reef slope, the impact (if any) of sharks on coral reef community structure is likely to be greater on the reef slope compared to other reef habitats, assuming that predation pressure is directly related to shark density. Further research is needed to validate this assumption as previous findings suggest that some reef sharks (i.e. *C. amblyrhynchos*) may acquire as much as ~80% of their nutrition from pelagic-based sources rather than reef-based sources, even though they were observed more on the forereef slope compared to other reef habitats (McCauley et al. 2012)

Though mechanisms responsible for habitat partitioning among reef sharks require further investigation, several factors may explain differences in shark density and diversity between habitats. Firstly, variation in habitat use may be due to predator avoidance. For instance, juvenile lemon sharks (*Negaprion brevirostris*) prefer shallow water mangrove habitats, possibly due to decreased predation risk (Morrissey and Gruber 1993). In the current study, only juvenile *N. ferrugineus* was observed on the reef flat, which provide some support for the predator avoidance hypothesis. Secondly, habitat quality may also explain differences in reef shark density and diversity on a local scale. It has been suggested that environmental factors such as live coral cover, depth, topography, temperature and water quality may influence the level of site fidelity of reef sharks (Wetherbee et al. 1997; Papastamatiou et al. 2009b; Vianna et al. 2013; Espinoza et al. 2014). Thirdly, and perhaps more likely, variation in shark density and diversity between habitats may be due to foraging activity. Reef sharks predominantly feed on teleost fishes and benthic organisms such as crustaceans and cephalopods (Randall, 1977; Lyle, 1987; Salini et al. 1992; Papastamatiou et al. 2006; Frisch and Rizzari unpubl data). Consequently, time spent foraging in a specific habitat is likely to vary according to the availability of potential prey. This has been observed at Palmyra Atoll in the Line Islands where it was found that *C. melanopterus* source the majority of their dietary carbon from the forereef slope (McCauley et al. 2012), which would potentially support higher abundances of potential prey. Furthermore, the foraging activity of *T. obesus* may be linked to habitat quality as this species is highly specialized at feeding on prey that shelter inside deep holes and crevices that are unattainable to other species (Randall 1977). Hence, the feeding behaviour of *T. obesus* may explain why this species was observed more often on structurally complex habitats such as the reef slope and back reef. Collectively, all sharks were observed in greater relative abundance on the reef slope. The reef slope also supported increased shark diversity. These patterns may result from an increase in the number and diversity of other organisms, such as potential prey, that typify reef slopes of the GBR (e.g. Cheal et al. 2012). However, it must be noted that due to small sample sizes, results from *C. melanopterus* and *N. ferrugineus* are indicative of trends only.

In the current study, habitat quality (i.e. coral cover and structural complexity) was not a significant influential variable in model selection. Coral cover and structural complexity were auto-correlated with habitat type, with coral cover and complexity highest on the reef slope and lowest in the reef flat. As such, reef flats will likely support fewer potential prey species of reef sharks (Papastamatiou et al. 2009a; Friedlander et al. 2010). The corresponding patterns in coral cover, structural complexity, shark density, and diversity support the hypothesis that habitat quality may influence the diversity and distribution of reef sharks. However, habitat partitioning as related to foraging activities among reef sharks is still unclear on the GBR. Considering the vulnerability of coral reef habitats (particularly areas of high coral cover such as the reef slope) to direct and indirect human impacts (Graham 2014), and projected increases in disturbances due to climate change, coral reefs of the future are likely to become increasingly degraded, characterized by low levels of live coral cover and low complexity. Although it is still difficult to directly link reduced structural complexity to changes in fish (or shark) productivity (Graham 2014), our results contribute to a growing body of literature that will enable us to better predict and understand how environmental degradation may influence reef shark populations.

Three considerations must be accounted for when interpreting our results. Firstly, the utility of UVC for counting large mobile predators is contentious due to the nature of an organism's behaviour (e.g. Ward-Paige et al. 2010; Bozec et al. 2011). Underwater visual census was chosen because of the non-invasive nature and the ability to rapidly assess reef shark populations. A recent study indicates that reef shark behaviour is not influenced by diver presence and that diver-based abundance estimates (i.e. 45-min timed-swims) are comparable to diver-independent surveys such as baited-remote-underwater-videos (BRUVs; Rizzari et al. 2014b). Secondly, another potential consideration is that the current study may not have completely sampled the range of shark biodiversity on coral reefs, and thus the resulting diversity estimates are only indicative. Rapid surveys of biodiversity need to use a combination of techniques (e.g. UVC, BRUVs and/or catch-mark-recapture), as some methods will fail to detect some of the more cryptic shark species. Lastly, this study was only conducted during daylight hours and at relatively shallow depths (<30m; due to SCUBA limitations). Previous studies have shown clear differences in daily attendance patterns and depth use of reef sharks, with some individuals expanding their habitat and depth use at night (e.g. McKibben and Nelson 1986; Chapman et al. 2007; Field et al. 2011; Barnett et al. 2012; Vianna et al. 2013). As such, there is a possibility that sharks could move to other sections of the reef at night. In light of these considerations, it is recommended that future studies use a combination of techniques for assessing biodiversity and habitat use of sharks on coral reefs that take into consideration diel activity and depth-use patterns. Additionally, it should be noted that abundance estimates derived from studies such as the current one are relative estimates only (not absolute) and thus should not be used as inputs into ecosystem models or biomass estimates (see Ward-Paige et al. 2010a).

In summary, reef sharks on outer-shelf reefs of the GBR do not display homogeneous habitat distributions. In particular, it appears that *C. amblyrhynchos* and *T. obesus* occupy the reef slope and back reef more than the reef flat, while *C. melanopterus* and *N. ferrugineus* occupy the reef flat more than the reef slope and back reef. In general, reef shark diversity and overall density was highest on the reef slope and lowest on the reef flat. Consequently, different habitats need to be considered whenever a comprehensive assessment of reef shark diversity and/or population size is required. In addition, our results highlight the potential importance of the reef slope, with high levels of live coral cover and structural complexity, for sustaining reef sharks. As this habitat is highly susceptible to disturbance events, this study provides a useful context for predicting and understanding how environmental degradation may influence reef shark populations in the future.

CHAPTER 4: Impact of conservation areas on trophic interactions between apex predators and herbivores on coral reefs

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4.1 Synopsis

Apex predators are declining at alarming rates due to exploitation by humans, but we have yet to fully discern the impacts of apex predator loss on ecosystem function. In a management context, it is critically important to clarify the role apex predators play in structuring populations of lower trophic levels. Thus, we examined the top-down influence of reef sharks (an apex predator on coral reefs) and mesopredators on large-bodied herbivores. We measured the abundance, size structure, and biomass of apex predators, mesopredators, and herbivores across fished, no-take, and no-entry management zones in the Great Barrier Reef Marine Park, Australia. Shark abundance and mesopredator size and biomass were higher in no-entry zones than in fished and no-take zones, which indicates the viability of strictly enforced human exclusion areas as tools for the conservation of predator communities. Changes in predator populations due to protection in no-entry zones did not have a discernible influence on the density, size, or biomass of different functional groups of herbivorous fishes. The lack of a relationship between predators and herbivores suggests that top-down forces may not play a strong role in regulating large-bodied herbivorous coral reef fish populations. Given this inconsistency with traditional ecological theories of trophic cascades, trophic structures on coral reefs may need to be reassessed to enable the establishment of appropriate and effective management regimes.

4.2 Introduction

Apex predators are facing declines across many of the world's ecosystems, largely as a result of persecution by humans (Treves and Karanth 2003). Changes in apex predator populations can release lower trophic levels from top-down control, leading to ecological changes that cascade through an entire ecosystem and subsequently alter community structure (Estes et al. 2011; Ripple et al. 2014). For example, the loss of wolves (*Canis lupus*) in Yellowstone National Park and declines in shark populations in the western North Atlantic have reportedly caused mesopredator release and trophic cascades (Berger and Conner 2008; Ferretti et al. 2010). Furthermore, changes in apex predator populations can also affect biodiversity patterns (Letnic et al. 2012), thereby potentially influencing functionally important herbivore populations and plant communities (Fortin et al. 2005; Ripple et al. 2013). Thus, the maintenance of healthy apex predator populations may contribute to biodiversity conservation (Sergio et al. 2006) and ecological stability (Ritchie et al. 2012). Although a popular topic for investigation (Estes et al. 2011; Ripple et al. 2014), our understanding of the roles played by apex predators is limited, particularly in the marine realm.

Sharks are common apex predators in marine ecosystems (Heithaus et al. 2008), but they are often the first removed during exploitation because of their high catchability and K-selected life-history traits (Stevens et al. 2000). This is particularly evident on coral reefs; recent research indicates widespread depletion of shark populations by fishing and other human activities (Robbins et al. 2006; Graham et al. 2010; Nadon et al. 2012). This is a major concern, because we have yet to fully understand the ecological roles of sharks on coral reefs or the consequences of their removal (Ceccarelli et al. 2014). Effective marine reserves can protect reef shark populations (Robbins et al. 2006; Heupel et al. 2009) and are increasingly advocated for fisheries management, conservation, and enhancing key ecosystem processes

(Graham et al. 2011; McClanahan et al. 2014). As such, marine reserves can be used as reference areas to quantify the detrimental effects of human activities, such as fishing (Graham et al. 2011).

The effect of changing apex predator densities on herbivorous fish assemblages is a large concern for coral reef managers. Herbivores perform a critical role on coral reefs by mediating the competition for space between corals and algae. Accordingly, declining herbivorous fish populations have resulted in the expansion of macroalgae in many reef systems (Hughes et al. 2007b; Rasher et al. 2013). While declines in herbivory have been linked to overfishing of herbivores themselves (Hughes et al. 2007a), similar responses may also manifest through changes in predator communities (e.g. Houk and Musburger 2013; Ruppert et al. 2013; Rizzari et al. 2014a). However, outputs of theoretical models provide contrasting evidence as to whether apex predators play a major (Bascompte et al. 2005) or minor (Stevens et al. 2000) role in trophic structuring on coral reefs. Furthermore, empirical investigations of the importance of apex predators are rare, probably due to the necessarily large sampling effort and wide geographic scales. The effects of changes in predator densities on herbivorous reef fish communities have been investigated (e.g. Friedlander and DeMartini 2002; Sandin et al. 2008; Houk and Musburger 2013; Ruppert et al. 2013), but these studies all treated herbivores as a single trophic group. This is problematic because there is considerable variation in feeding behavior among species, which reflects each species' functional role in ecosystem processes (Bellwood et al. 2006; Hoey et al. 2013). Therefore, it may be more appropriate to describe community-level patterns based on distinct herbivore functional groups (Green and Bellwood 2009), rather than broadly characterized trophic distinctions.

Demonstrating the top-down role of apex predators is exceedingly difficult because of the concomitant exploitation of fishes at lower trophic levels (Pauly et al. 1998) and the size-related demographically shifting roles of marine organisms (Trebilco et al. 2013). Because there is little to no capacity for experimental studies at such large spatial scales, ecologists inevitably must rely on natural experiments. The management zoning system of the Great Barrier Reef Marine Park (GBRMP) provides an appropriate setting in which to investigate the role of apex predators because it generates strong gradients in fishing pressure, which demonstrably influence predator populations (e.g. Robbins et al. 2006). The management system of the GBRMP includes no-entry zones, which are strictly enforced human exclusion areas; no-take zones, which are conservation areas where fishing is prohibited but non-extractive activities (e.g., diving) are allowed; and fished zones, which are general use areas permitting fishing and other extractive activities. Finally, herbivorous fishes are not typically targeted by fishers on the GBR. Thus, the GBR presents a unique opportunity to examine the effects of top-down trophic structuring on herbivore populations with minimal confounding effects. Our objectives were to examine how marine reserves influence the abundance, size structure, and biomass of both apex predator and mesopredator populations and explore the flow-on effects of marine reserve status and consequent changes in predator communities on herbivore community structure.

4.3 Methods

Study area and species

We assessed apex predator, mesopredator, and herbivore populations across 6 haphazardly selected locations spanning a latitudinal gradient of ~1000 km in the GBRMP (Fig. 4.1). Surveys were conducted from October through April (austral summer) over three years (2011-2013) to minimize seasonal variations. We surveyed six reefs per management zone (fished, no-take, and no-entry; total = 18). The duration of protection (reserve age) at

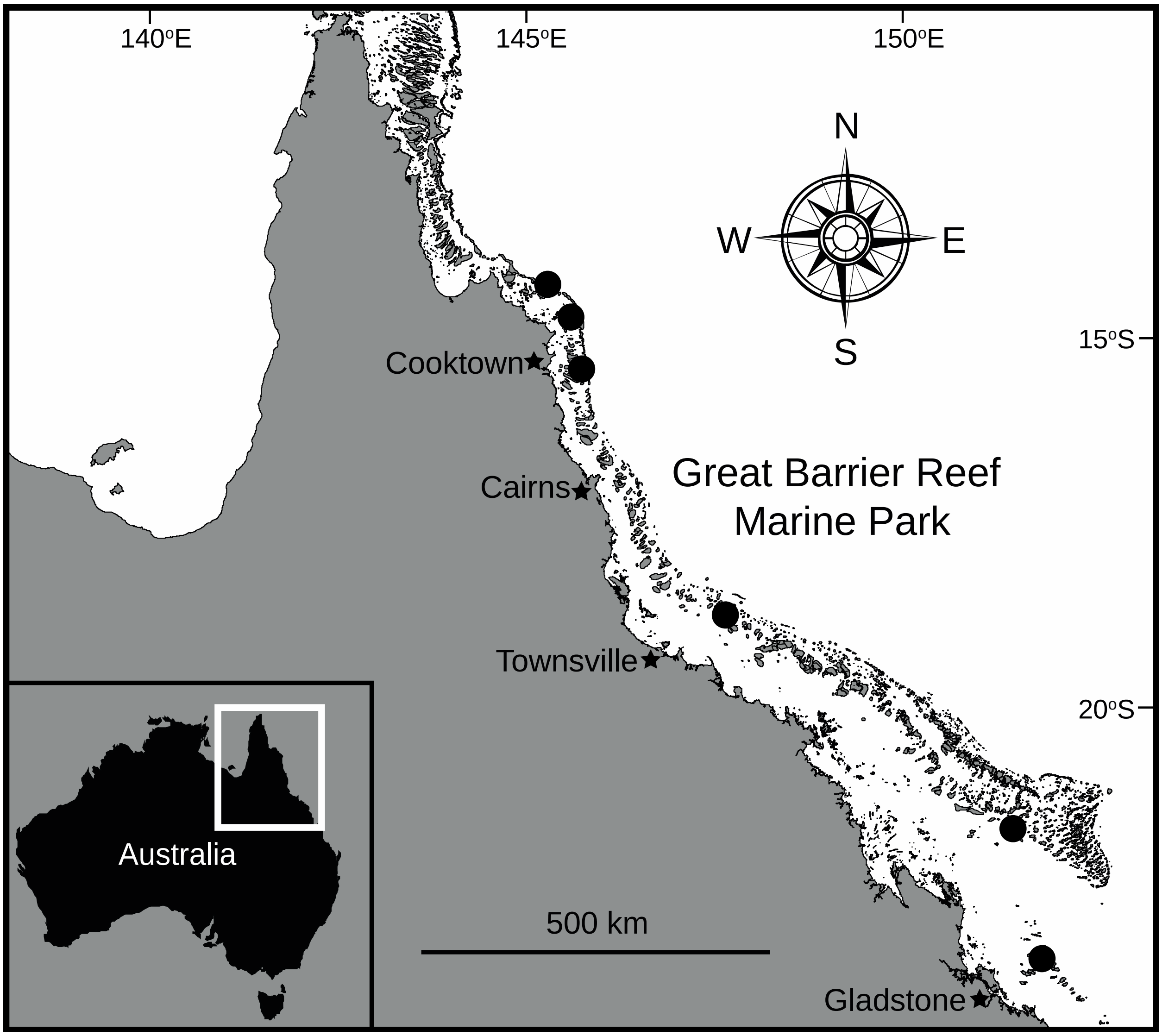


Fig. 4.1. Map of study locations (black circles) in the Great Barrier Reef Marine Park, Australia.

each reef varied from 0 to 34 years. Reefs were therefore grouped into three categories for subsequent analyses: zero years of protection (fished zones); 10-20 years of protection; or >20 years of protection (Table 4.1). Estimates of apex predator abundance were recorded for all reef-associated shark species. Three species (*Triaenodon obesus, Carcharhinus amblyrhynchos,* and *C. melanopterus)* were most abundant and classified as apex predators because they occupy the top trophic level of food webs on coral reefs (Speed et al. 2012). We split mesopredators into 2 categories: targeted (i.e. fished) or non-targeted. Targeted mesopredators included *Plectropomus leopardus*, *P. laevis*, *Lutjanus carponotatus*, and

Lethrinus miniautus, which are typically the most desirable species on the GBR (Frisch et al. 2012, 2014). Non-targeted mesopredators included all other species from the families Lethrinidae, Lutjanidae, and Serranidae. Herbivorous fishes included all species from the families Acanthuridae, Kyphosidae, Scaridae, and Siganidae. We categorized herbivores into one of three functional groups based on diet, feeding mode, and ecosystem role (Green and Bellwood 2009): scrapers and excavators; grazers and detritivores; and browsers. Scrapers and excavators feed primarily on the epilithic algal matrix (EAM), but they also remove parts of the underlying carbonate substratum. Grazers and detritivores also feed mostly on the EAM, but they typically do not remove the underlying substratum. Finally, browsers feed almost exclusively on fleshy macroalgae and associated epiphytic material.

Table 4.1. Information of each reef regarding years of protection and subsequent grouping for analysis purposes.

Management zone	Reef	Years protected	Grouping for analysis
Fished	Grub	0	0
	Hicks	0	0
	Herald's Prong 2	0	0
	Jewel	0	0
	No-name 15-043	0	0
No-take	Day	10	10-20
	Glow	27	>20
	Herald's Prong 3	10	10-20
	Lark	31	>20
	Tryon	10	10-20
	Yonge	10	10-20
No-entry	Arc	27	>20
	Bell Cay	10	10-20
	Carter	22	>20
	Hilder	22	>20
	Ribbon 6	31	>20
	Wreck	34	>20

Data collection

To quantify the abundance, size structure, and biomass of apex predators, mesopredators, and herbivores, we used underwater-visual-census (UVC) methods. All surveys were conducted on the reef slope at depths of 6 to 12 m; minimum visibility was 10 m. We chose the reef slope because the majority of reef sharks occupy this area (Robbins et al. 2006; Rizzari et al. 2014c), which consistently supports diverse reef fish communities within the GBR (Cheal et al. 2012).

Sharks were surveyed using 45-min timed swims, where a diver maintained a slow but steady swimming speed (~11 m/min) along the depth contour of the reef. This method is demonstrably robust for estimating reef shark abundance and has no associated biases as a result of shark behavior toward divers (Rizzari et al. 2014b). Sharks were counted only if they were ahead or within 10 m of either side of the observer (20 m transect width). A towed GPS unit enabled calculations of survey areas and standardization of count data to units of density. Two to six replicate surveys were performed at each reef. The mean survey length was 648.91 m (SE 16.62). Reduced replication was necessary at some reefs because of the large size of each survey relative to the size of each reef and the need for spatial separation of adjacent transects to ensure independence (replicates were separated by > 500 m). Time and identifying characteristics such as total length (TL), color patterns, and scars were recorded during shark observations to minimize the risk of pseudoreplication.

The abundance and biomass of mesopredators and herbivores were measured with a series of 50 m replicate transects. Ten to sixteen transects were conducted at each reef; adjacent surveys were separated by a minimum of 20 m. Each survey consisted of a diver following the depth contour of the reef and recording all mesopredators and herbivores >10 cm TL within a 10 m wide path (5 m on either side of the observer). A minimum size of 10 cm TL was selected to exclude juveniles, which are not amenable to rapid visual census methods (Hoey and Bellwood 2008). Care was taken not to re-survey fish that departed and subsequently reentered the transect area. In all cases, numbers per unit effort were converted to densities per hectare , and density estimates were converted to biomass (kilograms per hectare) with length-weight relationships (Froese and Pauly 2012).

Percent live coral cover and structural complexity were visually estimated in 10 m^2 areas at 5-minute intervals during apex predator surveys to investigate the effects of substrate on community structure. Structural complexity was categorized on a scale of one to five: 1, flat and sandy; 2, dominated by rubble, small rocks, algae, and encrusting corals but highly planar with few refuges; 3, abundant rocks or coral with limited three-dimensional structure but with occasional overhangs; 4, well-developed coral or rock structures with small overhangs but few large bommies (i.e. coral-covered outcrops) and caves; 5, multi-layered coral matrix with caves, large bommies, and abundant overhangs.

Data analysis

We investigated variation in the density, size, and biomass of apex predators, mesopredators, and herbivores with generalized linear mixed effects models (GLMM) with a log-link function. A negative-binomial error distribution was used for apex predator analyses to account for overdispersion, and all biomass data were log transformed. Substrate characteristics (i.e. coral cover and structural complexity) were also assessed using GLMMs. Separate GLMMs were performed for each trophic or /functional group. In all cases, management zone and years of protection were treated as fixed effects, whilst replicate transects were treated as random effects nested within reefs. Model selection was based on minimization of corrected Akaike information criterion (AICc), and the top two models (based on AICc values) are presented and detail the changes in AICc (ΔAICc) and model weights (wAICc). Parameter estimates and significance values are also presented for the top-ranked model for each trophic or functional group. We calculated non-parametric Spearman-rank correlation coefficients for all possible predator-prey combinations in each management zone to determine if predator and prey body size were related. We used a non-metric multidimensional scaling (nMDS) to explore variation among trophic groups between management zones. This analysis was based on the mean biomass per hectare of each trophic group at each reef. An additional nMDS was performed on the mean density of each trophic group at each reef to examine the relationship between density and biomass. Each nMDS was based on Bray-Curtis similarities of log-transformed data. The nMDS was performed with PRIMER version 6. All other statistical analyses were performed with R (R Development Core Team 2012).

4.4 Results

Model selection indicated that abundance patterns of apex predators, targeted mesopredators, and browsers were driven by the effect of management zone (Table 4.2). Non-targeted mesopredators were driven by years of protection, whilst the null model was selected at best predicting scraper and excavator and grazer and detritivore abundance (Table 4.2). This was also reflected in the GLMM: apex predator and browser density in no-entry zones were significantly greater than densities in no-take or fished zones (Fig. 4.2; Table 4.3). Model selection revealed that the effect of management zone and years of protection were important drivers for targeted and non-targeted mesopredator density, respectively, but these effects were not significant (Fig. 4.2; Table 4.3). Scraper and excavator and grazer and detritivore density appeared to be unrelated to management zone or changes in predator abundance (Fig. 4.2; Table 4.3).

In support of the null model, size and biomass were similar across management zones for all trophic groups, with the exception of both targeted and non-targeted mesopredators

(Fig. 4.3). Years of protection were identified in the top model (Table 4.2) as a significant predictor of size, and biomass, for both mesopredator groups (Table 4.3). Size and biomass of all herbivores appeared to be unrelated to management zone or changes in predator abundance, size, or biomass (Fig. 4.3; Table 4.3). Furthermore, there appeared to be no relationship between predator and prey body sizes across all three management zones (Fig. 4.4). Larger scrapers and excavators were observed in no-entry zones, but this pattern was not significant (Fig. 4.3e). The presence of larger scrapers and excavators in no-entry zones was driven solely by the presence of a single school of one species, *Bolbometopon muricatum*.

The nMDS analysis displayed a separation of no-entry zones from fished and no-take zones for both density (Fig. 4.5a) and biomass (Fig. 4.5b). No-entry zones contained higher densities of apex predators and browsers relative to no-take and fished zones (Fig. 4.5a). No-entry zones also contained greater biomass of apex predators, both mesopredator groups, and scrapers and excavators (Fig. 4.5b). Model selection indicated that percent coral cover was influenced by years of protection; however, this effect was not significant (Table 4.4; Fig. 4.6). Structural complexity was consistent across all three management zones and was described best by the null model (Table 4.4; Fig. 4.6).

Table 4.2. Results of generalized linear mixed models (GLMM) of abundance (number per hectare), size (total length in centimeters), and log-transformed biomass (kilograms per hectare) of 6 trophic groups relative to years of area protection and management zone protection.

Trophic group	Variable	Model[a]	df	logLik	AICc	ΔAICc	wAICc
Apex predators	abundance	zone[b]	6	-170.35	353.80	0.00	0.68
		zone + years protected	7	-169.94	355.35	1.55	0.31
	size	null	3	-1095.45	2197.00	0.00	0.52
		years protected	4	-1094.89	2197.93	0.93	0.33
	biomass	null	3	-217.69	441.50	0.00	0.50
		years protected	4	-217.01	442.21	0.71	0.35

Targeted mesopredators[c]	abundance	zone	6	-1288.71	2589.80	0.00	0.38
		zone + years protected	7	-1287.91	2590.34	0.54	0.29
	size	years protected	4	-1857.07	3722.20	0.00	0.54
		zone	5	-1856.91	3723.92	1.72	0.23
	biomass	years protected	4	-511.92	1031.90	0.00	0.52
		zone	5	-511.62	1033.34	1.44	0.25
Non-targeted mesopredators[c]	abundance	years protected	5	-1552.00	3114.30	0.00	0.46
		null	4	-1553.43	3115.07	0.77	0.31
	size	years protected	4	-4336.10	8680.20	0.00	0.58
		zone	5	-4335.93	8681.87	1.67	0.25
	biomass	years protected	4	-1243.04	2494.10	0.00	0.57
		zone	5	-1242.77	2495.57	1.47	0.27
Browsers	abundance	zone	6	-1676.89	3366.20	0.00	0.55
		zone + years protected	7	-1676.88	3368.31	2.11	0.19
	size	null	3	-8354.01	16714.00	0.00	0.63
		years protected	4	-8354.01	16716.01	2.01	0.23
	biomass	null	3	-2431.00	4868.00	0.00	0.62
		years protected	4	-2431.00	4870.01	2.01	0.23
Scrapers and excavators	abundance	null	4	-1656.62	3321.40	0.00	0.60
		years protected	5	-1656.62	3323.48	2.08	0.21
	size	null	3	-22499.76	45005.50	0.00	0.49
		years protected	4	-22499.18	45006.35	0.85	0.32
	biomass	null	3	-8477.89	16961.80	0.00	0.59
		years protected	4	-8477.74	16963.51	1.71	0.25
Grazers and detritivores	abundance	null	4	-1773.42	3555.00	0.00	0.40
		years protected	5	-1772.70	3555.66	0.66	0.29
	size	null	3	-22715.77	45437.50	0.00	0.54
		years protected	4	-22715.42	45438.82	1.32	0.28
	biomass	null	3	-7368.96	14743.90	0.00	0.56
		years protected	4	-7368.71	14745.39	1.49	0.26

[a] We assumed a negative binomial error distribution in models of apex predators to overcome overdispersion. Models presented are those with the 2 lowest values of Akaike information criterion (AICc). Abbreviations: logLik, model maximum log-likelihood; AICc, changes in AICc with respect to the top ranked model (ΔAICc) and AICc weights (wAICc). Significance values and parameter estimates of the top ranked model are presented in Table 2.

[b] Zone refers to the effect of management zone (i.e. fished, no-take, and no-entry).

[c] Targeted mesopredators are typically targeted for fishing whilst non-targeted mesopredators are not typically targeted for fishing.

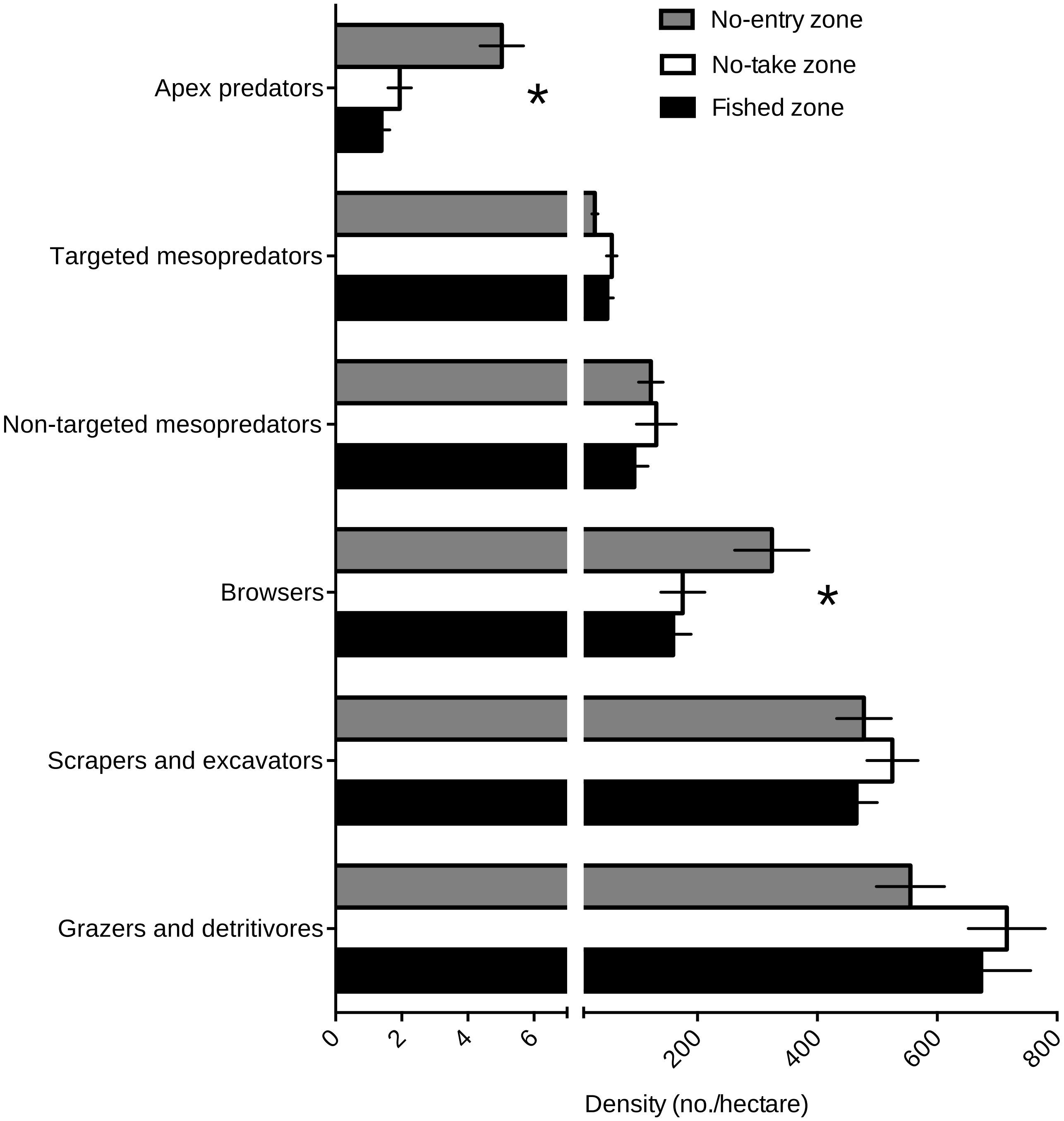


Fig. 4.2. Estimates of apex predator, targeted (i.e., fished) mesopredator, non-targeted mesopredator, browser, scraper and excavator, and grazer and detritivore density (lines, SE) across fished, no-take, and no-entry management zones. Asterisks indicate a significant effect of management zone identified by generalized linear mixed-effects models.

Table 4.3. Parameter estimates for the best-fitting generalized linear mixed-effects (GLMM) models of abundance (number per hectare), size (total length in centimeters), and log-transformed biomass (kilograms per hectare) of 6 trophic groups relative to years of area protection and management zone protection.

Trophic group	Variable	Effect[a]	Effect size estimate	df	SE	*t*	*p*
Apex predators	abundance	intercept	0.18	76	0.20	0.88	0.38
		zone (no-entry)	1.29	76	0.24	5.39	<0.0001[b]
		zone (no-take)	0.33	76	0.26	1.24	0.27
	size[c]	intercept	121.61	225	1.75	69.32	-
	biomass[c]	intercept	2.70	225	0.05	52.36	-
Targeted mesopredators[d]	abundance	intercept	49.74	209	8.16	6.09	<0.0001[b]
		zone (no-entry)	-20.79	209	11.54	-1.80	0.07
		zone (no-take)	7.33	209	11.58	0.63	0.53
	size	intercept	32.63	496	2.70	12.07	<0.0001[b]
		years protected	0.69	15	0.20	3.51	<0.01[b]
	biomass	intercept	2.42	496	0.14	17.43	<0.0001[b]
		years protected	0.04	15	0.01	4.14	<0.0001[b]
Non-targeted mesopredators[d]	abundance	intercept	85.40	210	23.59	3.62	<0.001[b]
		years protected	2.90	210	1.72	1.69	0.09
	size	intercept	30.64	1298	1.22	25.03	<0.01[b]
		years protected	0.24	18	0.08	2.88	0.01[b]
	biomass	intercept	2.24	1298	0.10	21.81	<0.0001[b]
		years protected	0.02	18	0.01	3.39	<0.01[b]
Browsers	abundance	intercept	159.47	209	45.13	3.53	<0.001[b]
		zone (no-entry)	164.74	209	63.82	2.58	0.011[b]
		zone (no-take)	16.26	209	64.03	0.25	0.8
	size[c]	intercept	37.37	2479	0.80	46.76	-
	biomass[c]	intercept	3.03	2479	0.07	42.44	-
Scrapers and excavators	abundance[c]	intercept	489.34	211	23.78	20.58	-
	size[c]	intercept	28.45	5536	1.21	23.60	-
	biomass[c]	intercept	2.00	5536	0.11	18.55	-
Grazers and detritivores	abundance[c]	intercept	647.93	211	39.77	16.29	-
	size[c]	intercept	26.13	7336	0.56	46.47	-
	biomass[c]	intercept	2.08	7336	0.06	33.62	-

[a] The intercept parameter corresponds to the predicted abundance per hectare, size (cm total length), or log(biomass; kilograms per hectare) in a fished zone. All other terms represent effect sizes.

[b] Significant at the 0.05 level.

[c] Null model was chosen during model selection (see Table 1).

[d] Targeted mesopredators are typically targeted for fishing whilst non-targeted mesopredators are not typically targeted for fishing.

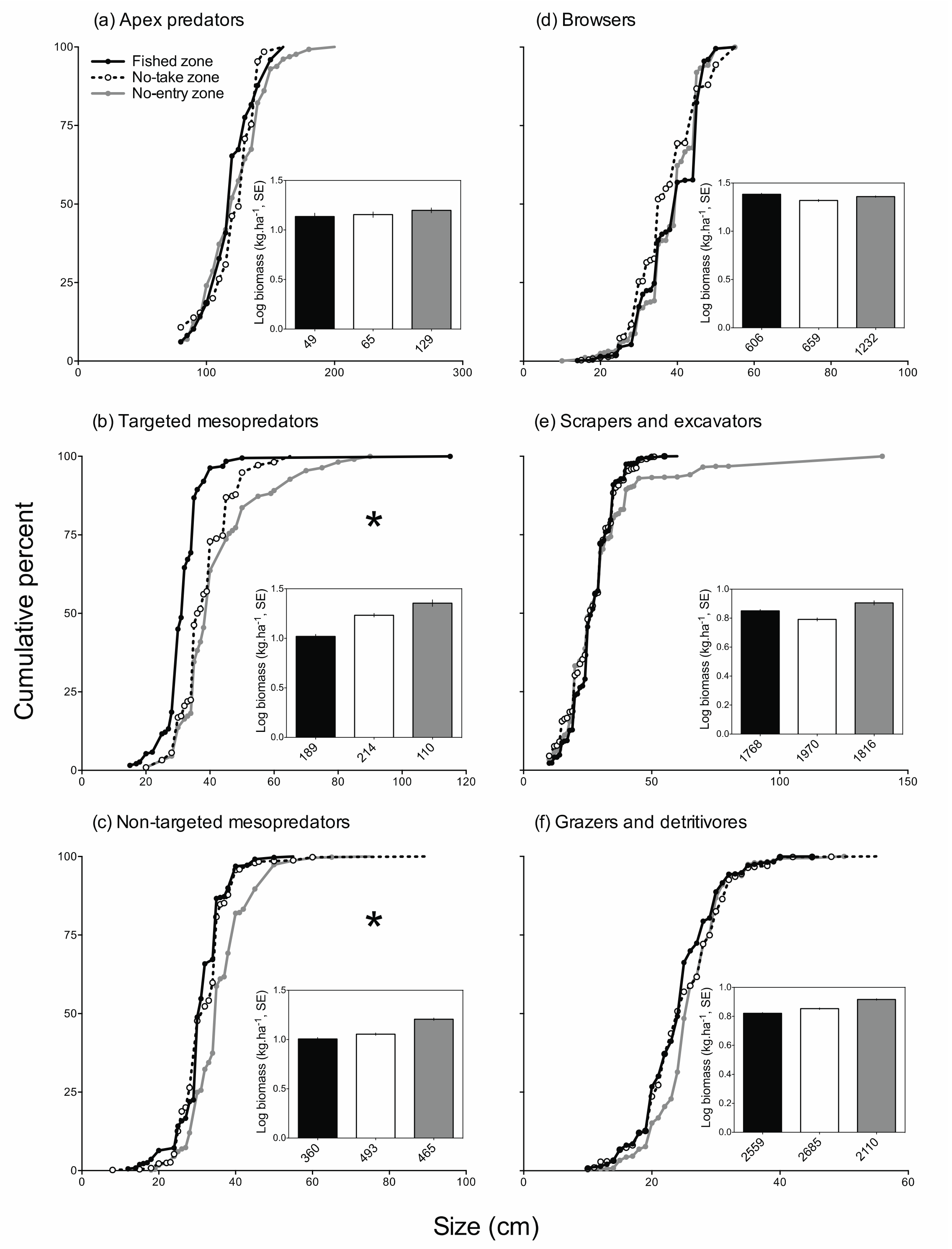
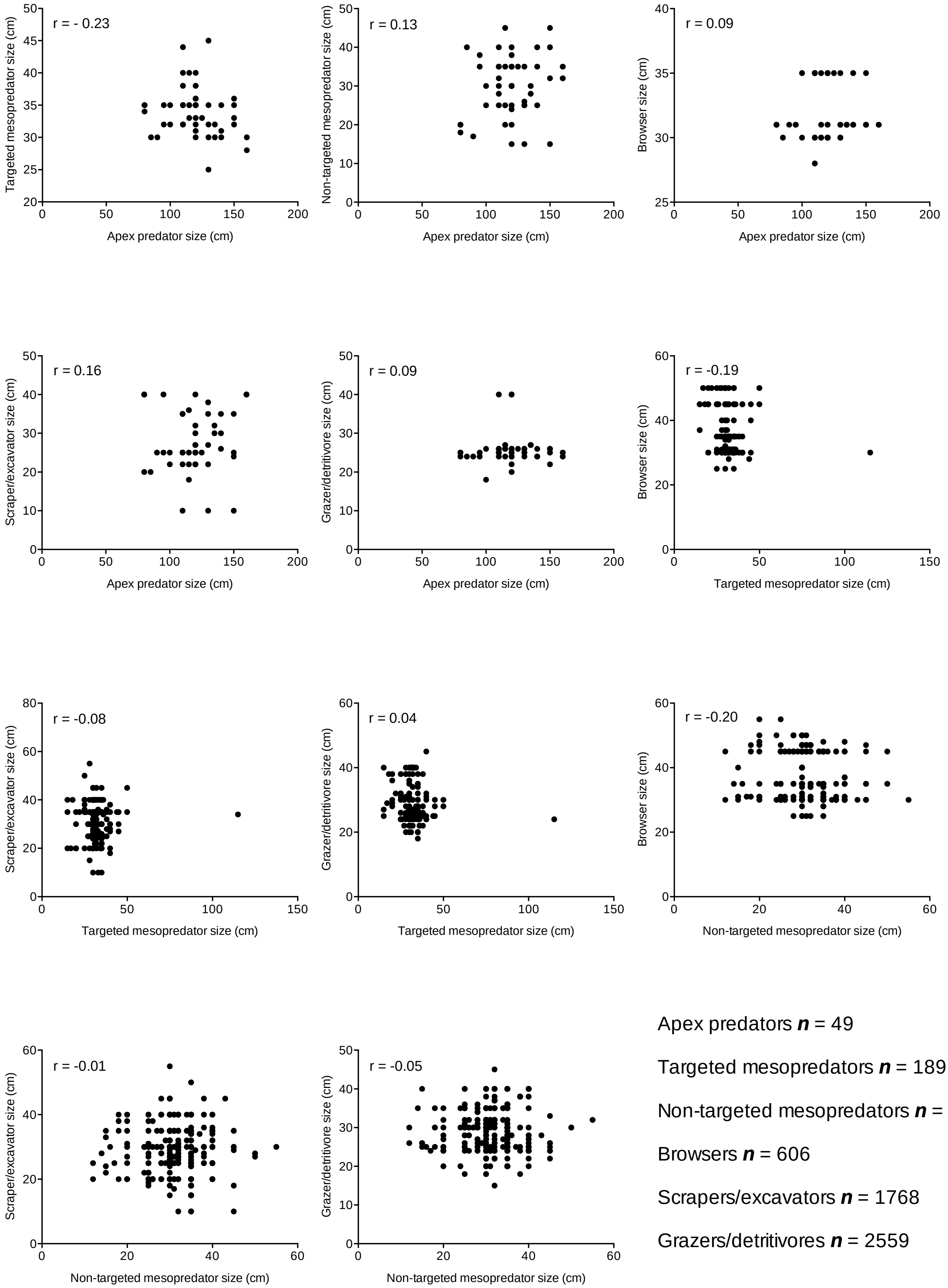


Fig. 4.3. Cumulative size-frequency distribution for (a) apex predators, (b) targeted (i.e., fished) mesopredators, (c) non-targeted mesopredators, (d) browsers, (e) scrapers and excavators, and (f) grazers and detritivores across fished (black line and solid black circle), no-take (dotted line and open circle), and no-entry (grey line and grey circle) magement zones. Inset of size-frequency distribution graph corresponds to each groups' log-transformed biomass across fished (black bars), no-take (white bars), and no-entry (grey bars) management zones. Numbers under bars are sample sizes for each group within each management zone. Asterisks indicate a significant effect of management zone (or years of protection) from generalized linear mixed-effects models.

(a) Fished zone



Apex predators ***n*** = 49

Targeted mesopredators ***n*** = 189

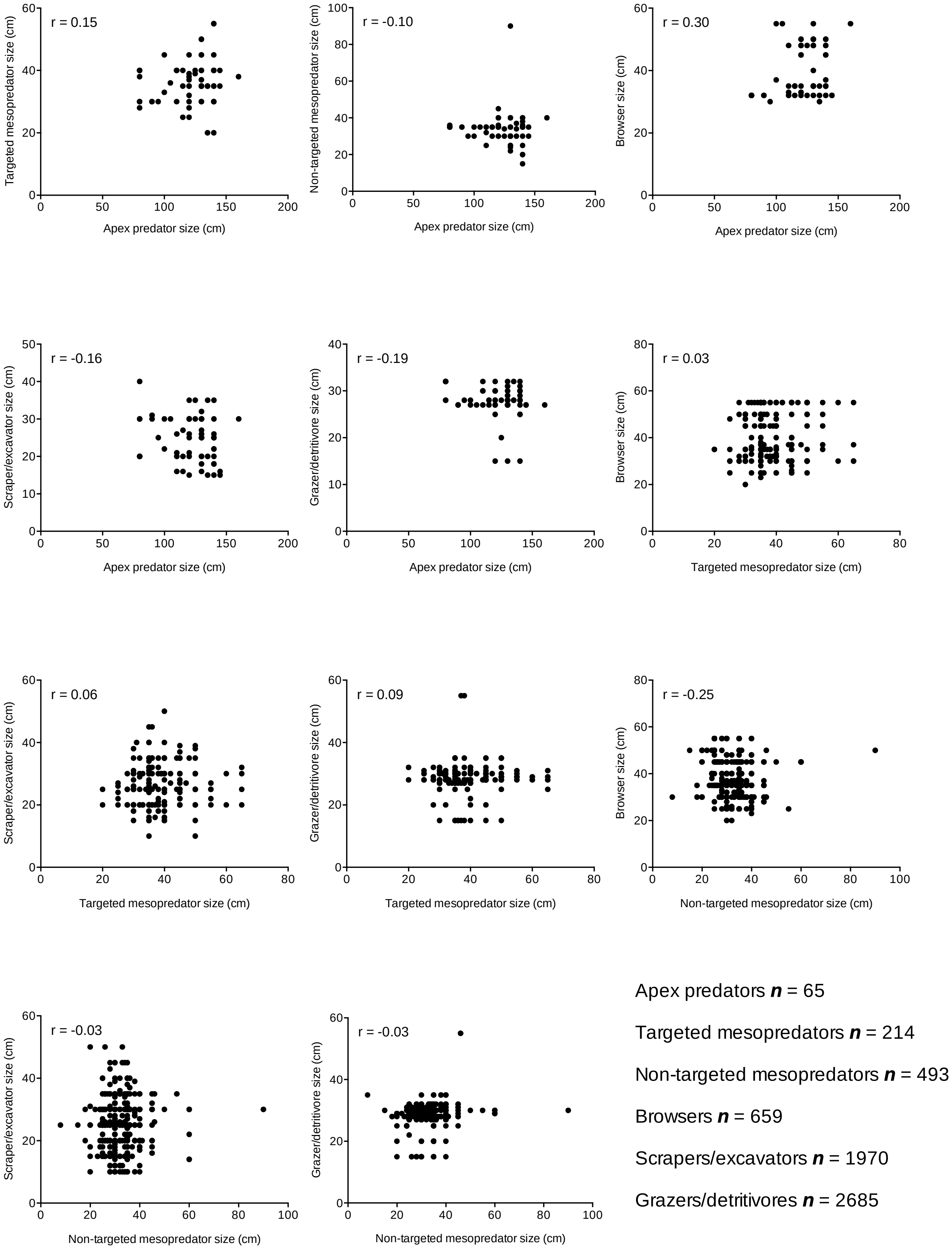
Non-targeted mesopredators ***n*** = 360

Browsers ***n*** = 606

Scrapers/excavators ***n*** = 1768

Grazers/detritivores ***n*** = 2559

(b) No-take zone



Apex predators ***n*** = 65

Targeted mesopredators ***n*** = 214

Non-targeted mesopredators ***n*** = 493

Browsers ***n*** = 659

Scrapers/excavators ***n*** = 1970

Grazers/detritivores ***n*** = 2685

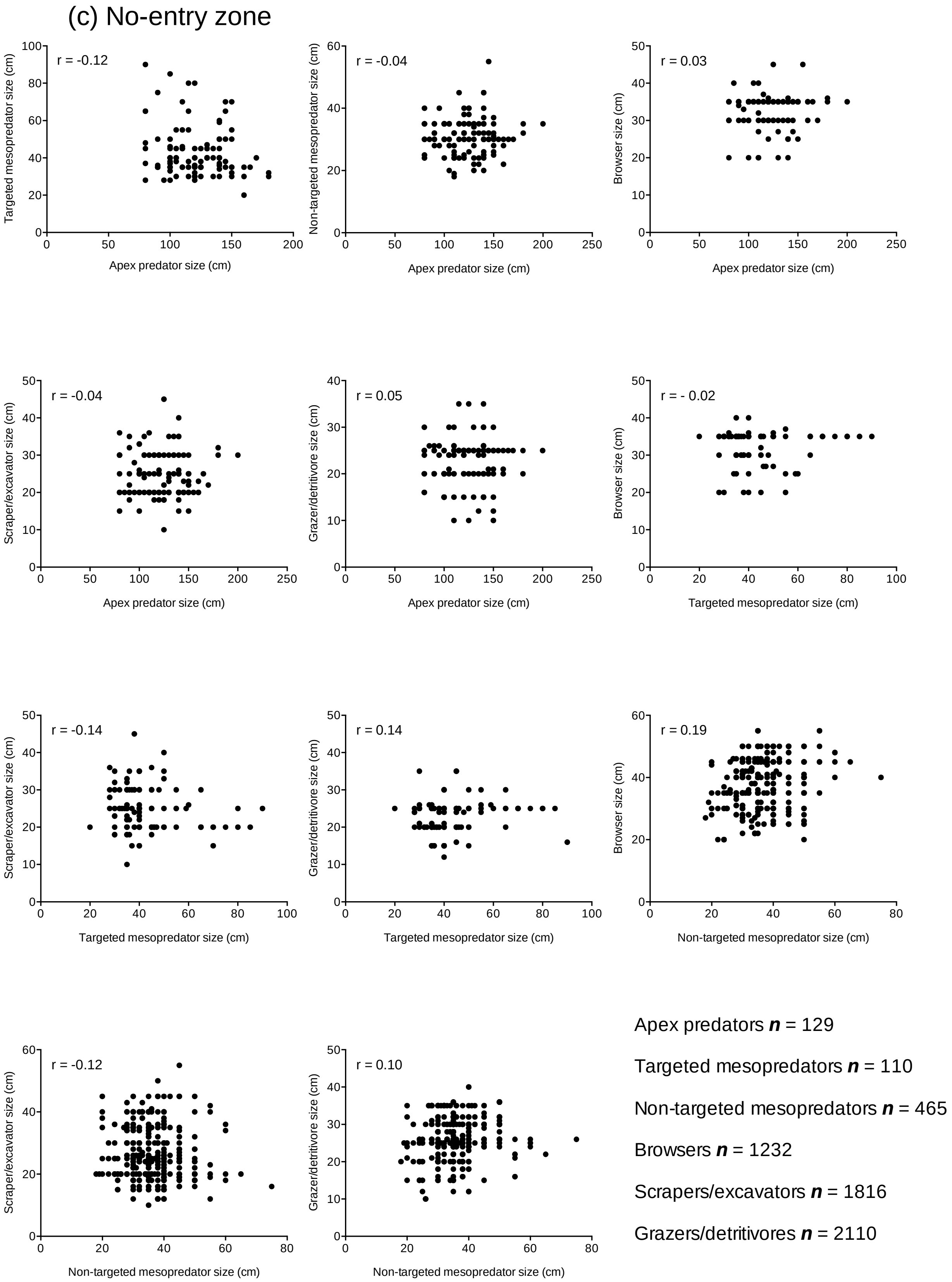


Fig. 4.4. Relationship between all combinations of predator and prey body sizes (cm total length, TL) in (a) fished zones (b) no-take zones and (c) no-entry zones. Shown are the correlation coefficients (top left) and the total number of individuals observed per trophic group (bottom right).

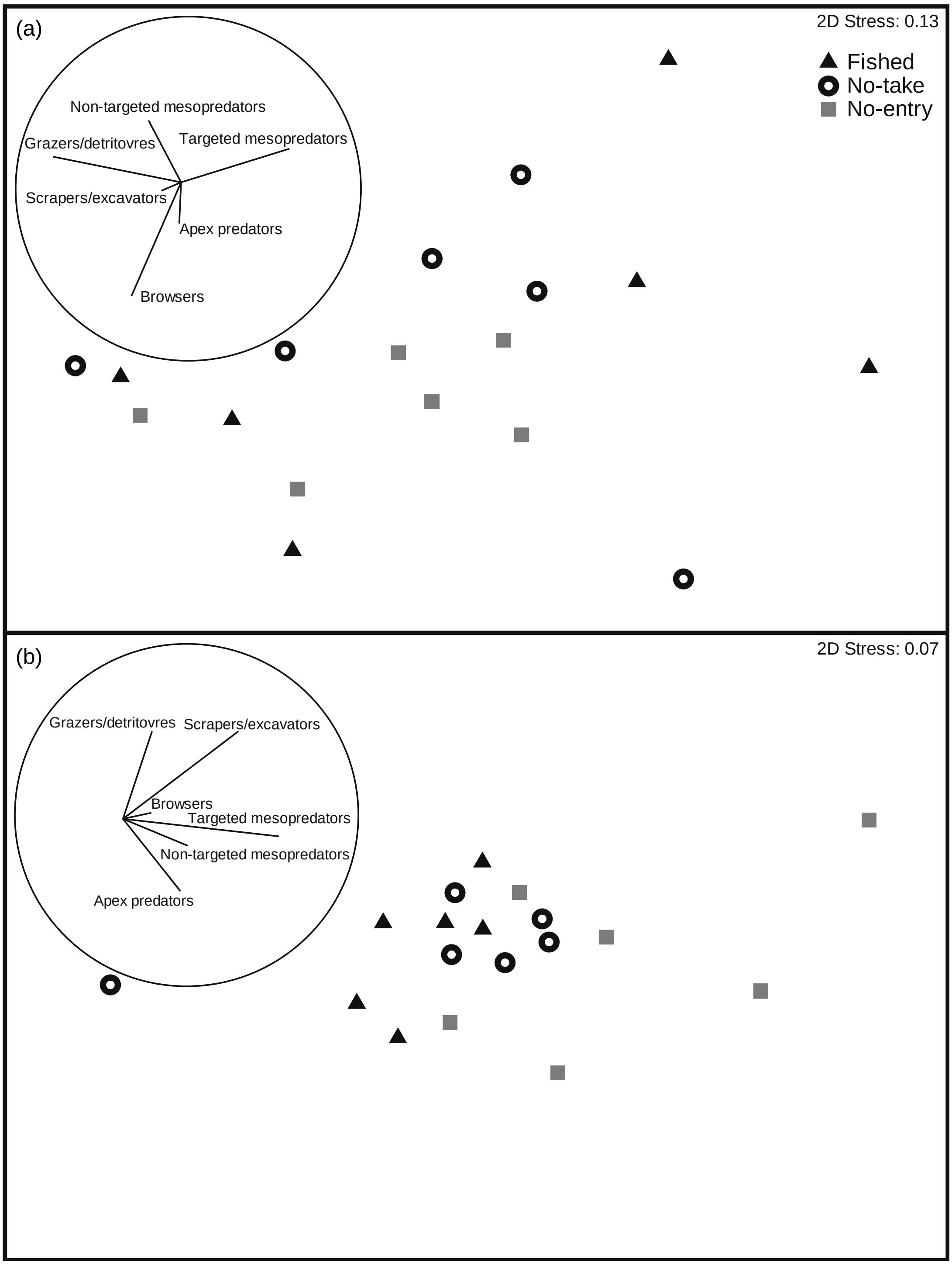


Fig. 4.5. Results of non-metric multidimensional scaling analyses performed on distance matrices for (a) density (number per hectare) and (b) biomass (kilograms per hectare) of trophic groups across fished (black triangles), no-take (open circles), and no-entry (grey squares) management zones. Targeted mesopredators refer to species typically targeted by fishers. Each analysis was based on Bray-Curtis similarities of $\log_{10}(x + 1)$ transformed data. Each reef is based on a minimum of 10 replicate transects (2 for apex predators). Vectors represent partial regression coefficients of the original variables (trophic groups) with the 2 dimensions. Lengths of the vectors are proportional to the squared multiple correlation coefficient.

Table 4.4. Summary of generalised linear mixed models (top half of table) and parameter estimates (bottom half of table) of the top model (**in bold**) for percent coral cover and structural complexity. Models presented are those with the two lowest values of Akaike information criterion (AICc). Shown are degrees of freedom (df), model maximum log-likelihood (logLik), AICc, changes in AICc with respect to the top ranked model (ΔAICc) and AICc weights (wAICc). Model parameter estimates (bottom half of table) of the top ranked model (**bold**) include effect sizes estimate, df, SE, test statistics and *p*-values (**in bold**) are significant at the 0.05 level. An asterisk and an unreported *p*-value indicate that the null model was chosen during model selection.

Habitat characteristic	Model	df	logLik	AICc	ΔAICc	wAICc
Coral cover	**Years protected**	5	-292.41	595.60	0.00	0.44
	Null	4	-294.01	596.54	0.94	0.28
Structural complexity	**Null**	4	-54.37	117.20	0.00	0.55
	Years protected	5	-54.35	119.42	2.22	0.18
	Effect	Estimate	df	SE	*t*-statistic	*p*
Coral cover	Intercept	16.86	77	1.32	12.78	**<0.0001**
	Years protected	-0.18	77	0.1	-1.78	0.08
Structural complexity*	Intercept	3.95	78	0.05	78.86	-

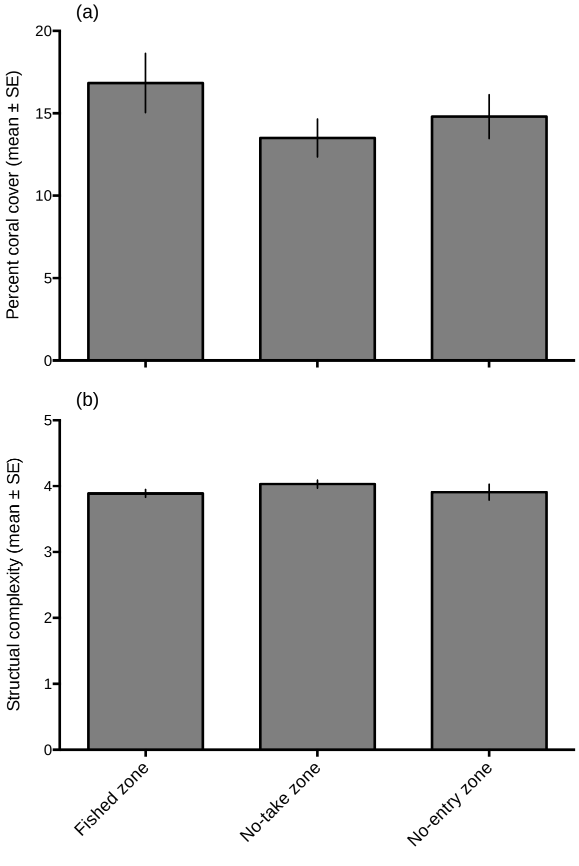


Fig. 4.6. Indices of habitat quality at fished, no-take and no-entry management zones on the Great Barrier Reef. (a) Percent live coral cover (mean ± standard error, SE), and (b) structural complexity (mean ± SE). Structural complexity metrics are defined in the Methods section.

4.5 Discussion

We found no evidence that top-down forces control herbivore populations. Specifically, changes in predator density and size, due to protection, had no discernible influence on large-bodied herbivorous fishes. These results are consistent with two other studies recently conducted in the northern GBR that demonstrate the limited (or no) influence of predation risk on the foraging behavior (Nash et al. 2012) or on home range sizes of large-bodied herbivorous parrotfishes (Welsh et al. 2013). Taken in light of these other findings, our results highlight the possibility that large-scale mechanisms shaping herbivorous fish populations on coral reefs may be regulated more by bottom-up rather than top-down forces (e.g. Smith et al. 2010).

Effective ecosystem-based conservation and management objectives are contingent upon a thorough understanding of trophic interactions (e.g. Treblico et al. 2013; Hussey et al. 2014a). However, a consensus has yet to be reached regarding the nature and strength of these interactions on coral reefs, particularly top-down forces. Recent studies examining the ecological role of apex predators, such as reef sharks, on coral reefs and their influence on lower trophic levels have generated inconsistent conclusions (Friedlander and DeMartini 2002; Sandin et al. 2008; Houk and Musburger 2013; Ruppert et al. 2013). All studies, including ours, demonstrate positive relationships between reef shark populations and/or protection status and degree of geographical isolation (i.e. human influence). However, observed changes in reef shark populations and the subsequent effects on herbivorous fishes vary considerably among studies. As in Sandin et al. (2008), we did not detect large-scale differences in herbivores across gradients of shark density. These findings contrast with other studies that demonstrate positive relationships between herbivore density or biomass (Friedlander and DeMartini 2002; Houk and Musbruger 2013; Ruppert et al. 2013) and shark populations. Given these disparate findings, further research is needed to fully elucidate the role of reef sharks as apex predators on coral reefs.

Reef shark density was highest in no-entry management zones. This pattern has been observed and attributed to poaching in no-take zones (Robbins et al. 2006). Relative to no-take zones, where fishing is prohibited, no-entry zones are strictly enforced exclusion areas, where even human presence is illegal. These zones are thus considerably easier to monitor and enforce than no-take zones, where enforcement personnel must produce legal evidence of poaching rather than a person's presence. Compliance is demonstrably critical for the efficacy of no-take zones (Edgar et al. 2014; Bergseth et al. 2015), and even low levels of poaching can remove effects of protection that often take decades to produce (Little et al. 2005). When combined with previous studies demonstrating low levels of poaching even within the most highly enforced sections of the GBRMP (i.e. near human population centers; Davis et al. 2004), our results suggest that levels of poaching in no-take areas of the GBR may be occuring at levels substantial enough to negate desired management outcomes.

The extent to which reef sharks affect coral reef food webs depends on their movement and residency patterns. Numerous studies demonstrate that most reef sharks exhibit high levels of site fidelity and remain on single reefs for long periods (Speed et al. 2011, 2012; Whitney et al. 2012; Vianna et al. 2013). Although reef sharks can move large distances, only a small proportion of individuals move between reefs (Heupel et al. 2010; Field et al. 2011; Barnett et al. 2012). As such, the trophic impact of reef sharks will be largely confined to a single reef. Nevertheless, some sharks may have obtained their energy sources from reefs outside of those surveyed in our study.

Mesopredator release theory stipulates that higher apex predator density should result in population declines of mesopredators and subsequent irruptions of herbivores due to decreased predation by mesopredators (Ritchie and Johnson 2009). Although we were fortuitous enough to examine trophic interactions in the absence of fishing pressure toward herbivores, the limitations of such a natural experiment do prevent us from unequivocally demonstrating the potential for mesopredator release. Sharks and other predatory fishes (i.e. targeted mesopredators) are simultaneously subject to fishing pressure outside protected areas on the GBR (as with many locations), thus potentially confounding the indirect effects of apex predators on lower trophic levels in fished zones. While no-entry zones may not be the perfect experimental controls, they are the closest alternative to an undisturbed coral reef ecosystem on the GBR.

Results from no-entry zones are inconsistent with mesopredator release theory because differences in shark densities were not associated with predicted changes in mesopredator or herbivore populations. This is even more surprising in light of previous research associating decreased reef shark populations with higher abundances of mesopredators and lower abundances of herbivores (Ruppert et al. 2013). The reasons for these contrasting results are unclear, but temporal and spatial differences between this study and Ruppert et al. (2013) may account for these differences. First, our study encompassed a larger spatial gradient, but it was more temporally limited. Second, the complexity of dietary interactions existing on coral reefs is likely to confound cross-ecosystem comparisons. For instance, mesopredators (. fishes from the families Lethrinidae, Lutjanidae, and Serranidae) typically do not form an important dietary component of reef sharks (Randall 1977; Papastamatiou et al. 2006; Chapter 6). Furthermore, a recent investigation of stable isotope information indicates that common mesopredators derive the majority of their diet from planktonic sources rather than herbivorous fishes (Frisch et al. 2014). Therefore, it seems unlikely that predation of reef sharks on mesopredators or predation of mesopredators on herbivores would substantially alter either of the two respective populations.

Two caveats apply to our interpretation of the mechanisms shaping herbivore populations. First, we assumed that shark density in no-entry zones is close to pre-exploitation levels or high enough to influence lower trophic levels. We are confident that shark densities are close to pre-exploitation levels in no-entry zones because some zones have been protected for upwards of 30 years and mean shark densities in no-entry zones are similar (within 30%) to historical-baseline estimates from other Indo-Pacific locations (Nadon et al. 2012). However, longer durations could be necessary to detect the effects of predator protection further down the food web. For example, tropical fisheries closures in Kenya resulted in a peak of total predator biomass after ~15-20 years, whereas the time scale of other functional groups varied over ~35 years and did not predictably follow successional theory (McClanahan 2014). Second, the temporally limited nature of our study is not conducive to the detection of bottom-up processes; many coral communities are in a constant state of fluctuation from natural disturbances that alter some fish assemblages in a bottom-up manner (Jones et al. 2004). While bottom-up processes could play a major role in shaping herbivore populations, our objectives were to examine the effects of top-down forces. We found no evidence to support the notion that top-down forces strongly regulate large-bodied herbivore populations on the GBR.

Step changes in body size can also influence predator-prey trophic interactions (Trebilco et al. 2013). For example, apex predators may be functional mesopredators before attaining maturity due to ontogenetic diet shifts (e.g. Scharf et al. 2000). Many predatory fishes are gape limited (i.e. they cannot consume prey larger than their mouth), and gape size scales with body size. Our results indicate that predator body size did not strongly influence large-bodied herbivore populations. Multiple lines of evidence support this hypothesis. First, shark size and biomass were consistent across management zones, indicating that any influence of body size (or gape limitation) would have remained consistent across all locations. Second, there was no detectable relationship between predator and prey body sizes. Finally, not all predators are gape limited; some shark species are capable of cutting their prey into pieces (Lucifora et al. 2009), thereby overcoming gape limitation. Our results indicate that a reclassification of trophic groups on the GBR is warranted. A topic of recent interest is the role of larger, transient sharks (e.g., tiger, bull, silvertip, and hammerhead) as apex predators on coral reefs. Moreover, a recent review suggests that reef sharks may be more aptly categorized as mesopredators (Heupel et al. 2014). Therefore, investigations of top-down forces on coral reefs should aim to determine the role and extent that larger, more mobile sharks play in structuring coral reef food webs and the degree of dietary overlap between reef sharks and other large predatory fishes.

Irrespective of the processes involved, the absence of a link between predators and herbivores has important implications for coral reef conservation and management. Current management regimes addressing only top-down forces may therefore inadequately protect ecosystem function. Overall, our results suggest that top-down forces do not play a strong role in regulating populations of large-bodied herbivorous fishes. A sound understanding of trophic interactions underpins our ability to accurately predict ecosystem responses to change. It appears that traditional trophic theories adopted from terrestrial realms are not applicable to all ecosystems; thus, our findings add credence to the call for a restructuing of marine food webs (Hussey et al. 2014a). Future research would benefit from an increased understanding of how reef organisms interact with each other and how energy is transferred throughout the ecosystem. Such information is vital if we are to provide accurate scientific information to managers and policy makers.

CHAPTER 5: Not worth the risk: apex predators suppress herbivory on coral reefs

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5.1 Synopsis

Apex predators are known to exert strong ecological effects, either through direct or indirect predator-prey interactions. Indirect interactions have the potential to influence ecological communities more than direct interactions as indirect effects are propagated throughout the population as opposed to only one individual. Indirect effects of apex predators are well documented in terrestrial environments, however there is a paucity of information for marine environments. Furthermore, manipulative studies, as opposed to correlative observations, isolating apex predator effects are lacking. Coral reefs are one of the most diverse ecosystems, providing a useful model system for investigating the ecological role of apex predators and their influence on lower trophic levels. Using predator models and transplanted macroalgae we examined the indirect effects of predators on herbivore foraging behaviour. We show that the presence of a model reef shark or large coral-grouper led to a substantial reduction in bite rate and species richness of herbivorous fishes and an almost absolute localized cessation of macroagal removal, due to the perceived risk of predation. A smaller-sized coral-grouper also reduced herbivore diversity and activity but to a lesser degree than the larger model predators. These indirect effects of apex predators on the foraging behaviour of herbivores may have flow-on effects on the biomass and distribution of macroalgae, and the functioning of coral reef ecosystems. This highlights that the ecological interactions and processes that contribute to ecosystem resilience may be more complex than previously assumed.

5.2 Introduction

Predation is arguably one of the most influential selection pressures acting on living organisms and can play a vital role in not only regulating prey populations, but also shaping entire communities (Paine 1966; Hixon et al. 2002). In particular, changes in the density and distribution of large-bodied or apex predators can exert strong ecological effects that cascade through an entire ecosystem (e.g. Estes et al. 1998; Ripple et al. 2001; Frank 2008; Sandin et al. 2008; Estes et al. 2011; Ripple et al. 2013). Apex predators are typically characterized by conservative life history traits, such as slow growth rates, late sexual maturity, and low fecundity, and are often preferentially targeted by humans for food or game (e.g. Pauly et al. 1998; Myers and Worm 2003). Consequently, apex predators are often the first to be become extinct or locally extirpated. Understanding the roles that apex, and other large-bodied predators play in shaping ecological communities is becoming increasingly important as natural communities become progressively more disturbed.

The effects of predators on ecological communities may manifest through either direct (i.e. consumptive) or indirect (i.e. non-consumptive) interactions (for review see Schmitz et al. 2004). Although studies reporting direct effects of predators on ecosystems are common (e.g. Estes et al. 1998; Ripple et al. 2013), there is a growing body of evidence that the indirect effects of predators can have an equally dramatic effect on the structure and functioning of entire ecosystems (e.g. Preisser et al. 2005; Creel and Christianson 2008; Madin et al. 2010a). Given the severe consequences that a predation event poses, prey are under considerable pressure to successfully detect and avoid predators. Prey species often alter their behaviour and/or foraging patterns in response to changes in predation risk, and this in turn may influence the distribution and/or abundance of the prey's resources (Ripple et al. 2001; 2013). In particular, increased predation risk indirectly influences the foraging patterns of herbivores, which can lead to changes in plant diversity, productivity, nutrient cycling, trophic transfer efficiency and energy flux (Schmitz et al. 2008). For example, African herbivores change their habitat preference to more open habitats when in the presence of predatory lions, presumably as a response to the increased ability to detect predators in these areas (Valeix et al. 2009). Similarly, increased populations of wolves and other large carnivores in Yellowstone National Park reduced and redistributed herbivorous elk populations, subsequently decreasing herbivory and increasing tree height in high predation risk areas (Fortin et al. 2005; Ripple et al. 2013). Although these indirect predator-prey interactions are ubiquitous in ecological communities (e.g. terrestrial: Rypstra and Buddle 2012; aquatic: Peacor and Werner 2001; marine: Frid et al. 2012), there is a paucity of information on the effects of large-bodied or apex predators in tropical marine ecosystems (but see Madin et al. 2010a).

Coral reefs are one of the world's most taxonomically diverse ecosystems, harboring approximately 5,000 species of fishes that perform numerous functions and create a complex network of species interactions (Sheppard et al. 2009). Worldwide, overfishing and habitat degradation has greatly contributed to the decline of reef fish populations (Jackson et al. 2001), particularly apex predators such as reef sharks (family Carcharhinidae), groupers (family Serranidae) and trevally (family Carangidae) (Friedlander and DeMartini 2002, Robbins et al. 2006; Nadon et al. 2012). The contribution of apex predators to the well being of coral reef ecosystems is unclear, but is potentially important (Heithaus et al. 2008; Ruppert et al. 2013). For instance, differences in population parameters (e.g. size, longevity, reproduction and body condition) of prey fishes (Ruttenberg et al. 2011; Walsh et al. 2012), and rates of coral recruitment and disease (Sandin et al. 2008) have been correlated to variation in apex predator density, however little experimental evidence exists (see Madin et al. 2010a for exception). Thus, a better understanding of apex predators and their ecological role is imperative for guiding management actions that aim to preserve or enhance ecosystem resilience.

Herbivorous fishes perform a critical ecosystem function on coral reefs, mediating the competition for space between corals and algae. Reductions in the densities of herbivorous fishes underpin the expansion of macroalgae in many reef systems (Hughes et al. 2007b; Rasher et al. 2013). While such reductions in herbivory have been linked to overfishing of the herbivores themselves (Williams and Polunin 2001; Mumby et al. 2007), similar responses may manifest through changes in predator communities (e.g. Ruppert et al. 2013). Outputs of theoretical models suggest that changes in apex predator density could indirectly influence macroalgal biomass via mesopredator release and/or changes in prey behaviour (Bascompte et al. 2005). Two previous studies examining the effects of predators on herbivores revealed that differences in foraging behaviour (i.e. distance from shelter) were related to predator densities (Madin et al. 2010a, 2012), however no study has demonstrated a causal relationship between predators, herbivore foraging activity and algae consumption. Therefore, the present study aimed to investigate the effects of apex predators on the foraging behaviour of herbivorous reef fishes. Specifically, we examined the effect of predator presence on the consumption of macroalgae by herbivorous fishes. We selected the blacktip reef shark (*Carcharhinus melanopterus*) and the coral-grouper (*Plectropomus leopardus*) as model apex predator species because they occupy high trophic positions (Speed et al. 2012; Frisch et al. 2013), are numerically common, geographically widespread, have a broad diet that includes herbivorous fishes (Stevens 1984; St. John 1999) and are harvested across their geographic range by fishers (Frisch et al. 2012).

5.3 Methods

Study site and species

The study was conducted during November and December 2012 on reefs adjacent to Lizard Island (14°40'S, 145°28'E) in the northern Great Barrier Reef (GBR), Australia (Fig. 5.1). To quantify the effect of predators on the consumption of macroalgae, bioassays of *Sargassum* were transplanted to two sites both in the presence and absence of model predators. *Sargassum* was selected as it is locally abundant on inshore reefs of the GBR, has been used extensively in previous studies (e.g. McCook 1996; Hoey and Bellwood 2010), and is the dominant taxon following coral-algal phase-shifts on Indo-Pacific reefs (Hughes et al. 2007; Rasher et al. 2013). Model predator species included the coral-grouper and the blacktip reef shark. Coral-grouper hover over reefs near schools of prey for long periods, while blacktip reef sharks are more mobile. Both species are known to have small to moderate home ranges and exhibit high levels of site fidelity (Zeller 1997; Papastamatiou et al. 2011).

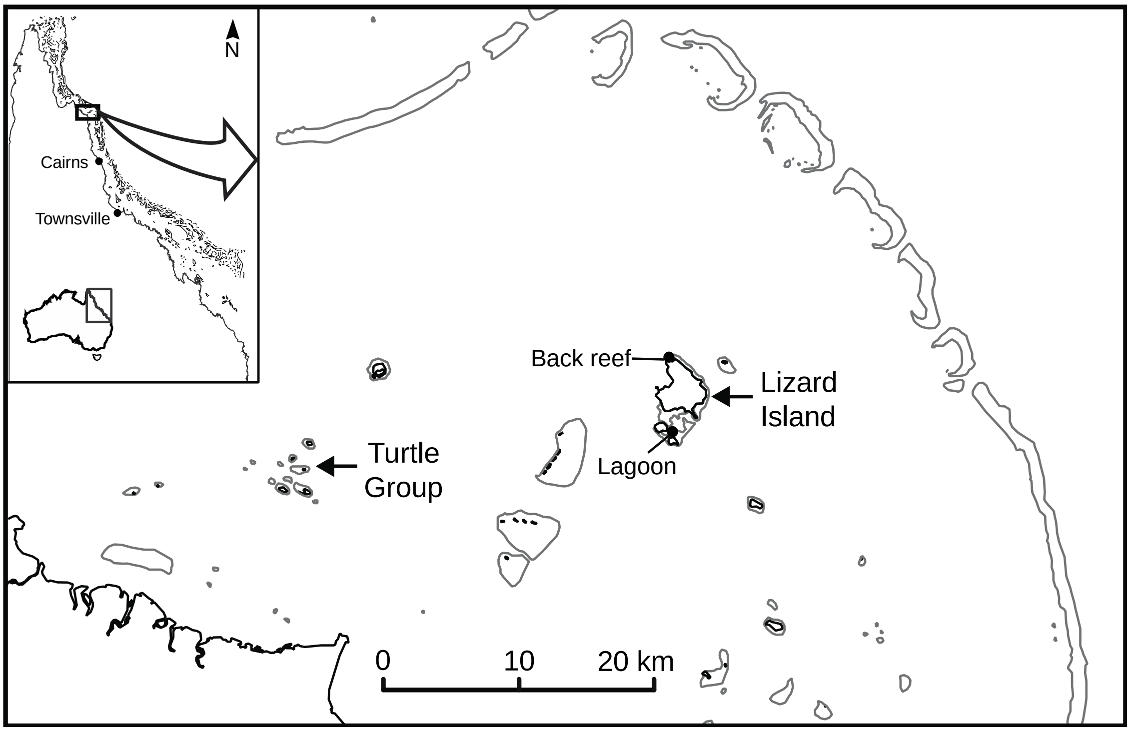

Fig. 5.1. Map of the Great Barrier Reef (GBR) showing the location of the study sites at Lizard Island and location of the Turtle Group, the site of collection of *Sargassum*.

Experimental design

Sargassum swartzii (Ochrophyta: Phaeophyceae) was collected from the windward reef flat of inshore reefs in the Turtle Island Group (14°43’S, 145°212’E), approximately 25 km west of Lizard Island (Fig. 5.1). Individual *Sargassum* thalli of similar height (*c.* 50 cm) were removed by cutting the holdfast as close to the point of attachment as possible. All *Sargassum* were returned to Lizard Island and placed in a large aquarium with flow-through seawater within 90 min of collection. Individual *Sargassum* thalli were spun in a mesh bag for 30 s to remove excess water, weighed (mean = 79.2 g ± 2.9 standard error, SE) and randomly allocated to one of six treatments: three predator treatments, a predator-absent treatment, an object control, and a herbivore exclusion control. To test the effect of predator presence on herbivory, we used realistic models constructed of fiberglass taxidermic casings (Fig. 5.2). Three predator-present treatments consisted of a blacktip reef shark (170 cm total length, TL), a large coral-grouper (76 cm TL) or a small coral-grouper (48 cm TL). Three different sized predators were used to simulate a gradient in predation risk (i.e. high for the reef shark, medium for the large coral-grouper and low for the small coral-grouper). During a pilot study, the small coral-grouper was attacked by a giant trevally (*Caranx ignobolis*) and investigated by a whitetip reef shark (*Triaenodon obesus*) suggesting that replicate models were perceived as life-like representations. The predator-absent treatment consisted of a *Sargassum* thallus in the absence of a predator model in order to obtain ‘natural’ rates of herbivory. The object control was a 78 cm length of PVC pipe (12 cm diameter), which was intended to control for the effect of any object on herbivore foraging behaviour. An exclusion cage was used to control for the effects of handling and/or translocation on the reduction in *Sargassum* biomass. Each treatment was replicated ten times within each of two sites; a lagoon and a back reef site (Fig. 5.1). Replicate treatments were conducted over a 30-day period and the location of each treatment, within each site, was randomized from day to day.

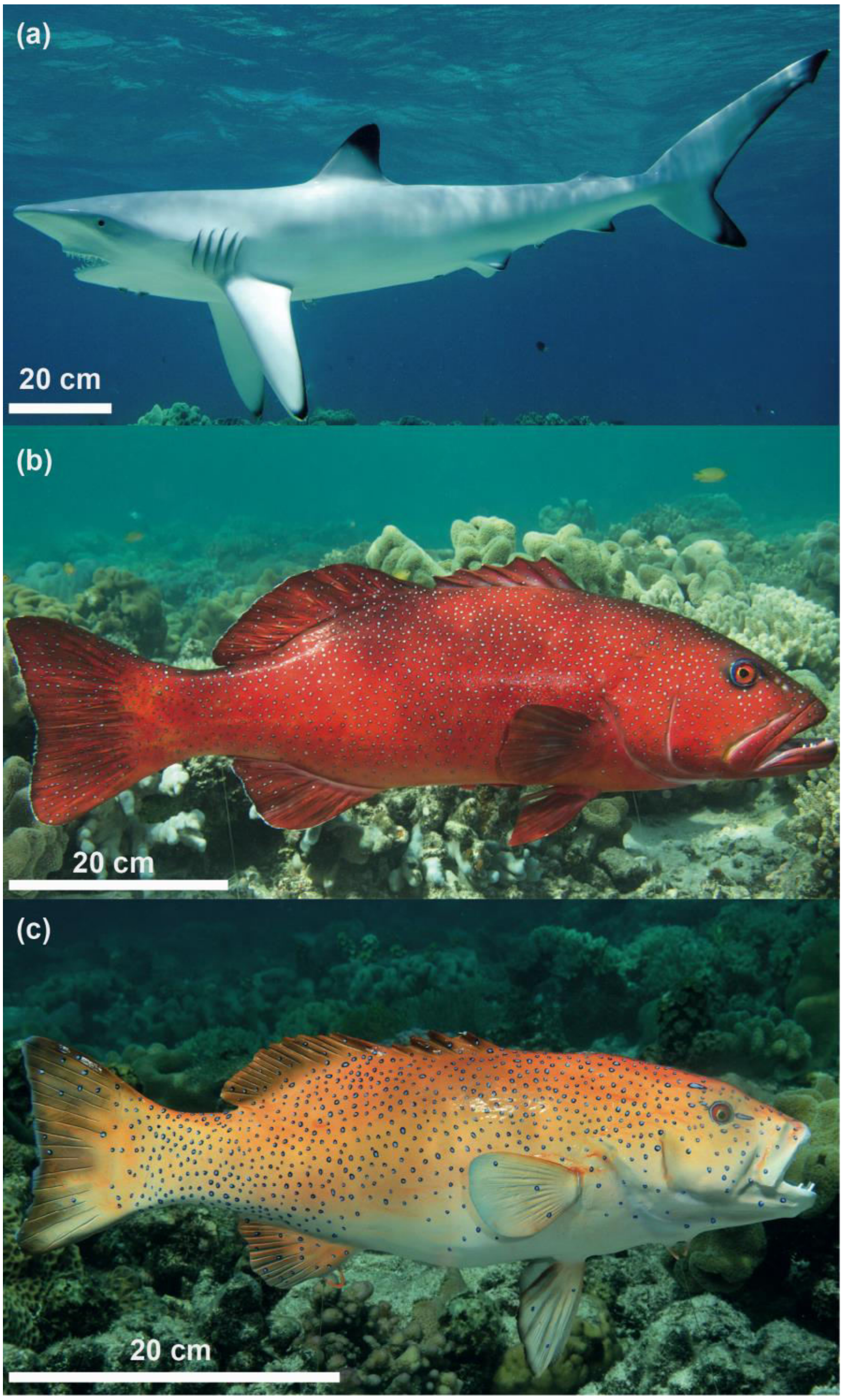

Fig. 5.2. Photographs of the three predator models. (a) Blacktip reef shark, *Carcaharinus melanopterus* (170 cm total length), (b) large coral-grouper, *Plectropomus leopardus* (76 cm total length), and (c) small coral-grouper, *P. leopardus* (48 cm total length).

Individual *Sargassum* thalli were attached to the reef at a depth of 2-4 m (following the methods of Hoey and Bellwood 2009), and positioned approximately 0.5-1 m in front of model predators (and object control). All *Sargassum* thalli were deployed between 0900-1100 and collected after 4.5 hours. A minimum distance of 50 m separated adjacent treatments within each site. Underwater video cameras (GoPro, Woodman Labs Inc.) were placed approximately 3 m from the *Sargassum* to record any feeding activity by herbivorous fishes. Filming was continuous for the 4.5-hour experimental period with a small scale bar being placed on the focal plane of the *Sargassum* for approximately 10 s allowing calibration of fish sizes from the video footage. After 4.5 h, all thalli were collected, spun and weighed as described previously. Filming was conducted at four of the six treatments (i.e. reef shark, large coral-grouper, small coral-grouper and predator-absent treatment); the exclusion cage and object control were not filmed as these treatments were established solely to examine the effects of handling and experimental artifacts, respectively. All video footage was viewed and the number of bites taken from the *Sargassum* by each species and size of fishes was recorded.

Statistical analyses

To determine if the relative removal rates of *Sargassum* biomass varied among sites and treatments, a two-factor analysis of variance (ANOVA) was used. The analysis was based on the proportion of initial (or transplanted) biomass that was removed during 4.5 h on the reef. Similarly, the total number of bites taken from the *Sargassum* (for all species combined) was compared amongst sites and treatments using a two-factor ANOVA. The proportion of biomass removed and total bites were arcsine-square root and $\log_{10}(x + 1)$ transformed, respectively, to improve normality and homoscedasticity. ANOVAs were followed by Tukey HSD *post hoc* tests to resolve differences between means. Variation in bite rate of different herbivorous fish species among sites and treatments was analysed using a two-factor multivariate analysis of variance (MANOVA). Data was $\log_{10}(x + 1)$

transformed to improve multivariate normality. Significant MANOVA effects were further examined using Bonferroni-corrected two-factor ANOVAs (adjusted alpha value of 0.0125) and Tukey HSD *post hoc* tests. A two-sample Kolmogorov-Smirnov test was used to examine the size-frequency distributions of herbivorous fishes observed feeding on *Sargassum* between treatments at both sites. In all cases assumptions of normality and homogeneity of variances were examined *a priori* via residual analysis and Bartlett's test, respectively. All data in the text and figures are the untransformed arithmetic mean (± standard error; SE) unless otherwise stated.

5.4 Results

The relative removal rates of *Sargassum* differed among sites ($F_{1,108} = 11.05$, $P = 0.001$) and predator treatments ($F_{5,108} = 50.05$, $P < 0.001$), with the effect of predator treatment being consistent among sites (site × predator treatment: $F_{5,108} = 2.03$, $P = 0.08$). In the absence of a model predator, or in the presence of the object control, the majority of *Sargassum* biomass was consumed (57-60 %) in the 4.5 h period (Fig. 5.3). There was, however, a ten-fold reduction in the *Sargassum* biomass consumed in the presence of the two larger predator models at both sites (5-6 % 4.5 h^{-1}; Fig. 5.3). Removal rates of *Sargassum* in the presence of a small coral-grouper model were intermediate, with 51 and 24 % 4.5 h^{-1} removed from the lagoon and back reef respectively. Reductions in *Sargassum* biomass due to handling were low (5 % 4.5 h^{-1}) and indistinguishable from the large coral-grouper and reef shark treatments (Fig. 5.3).

Analysis of the video footage revealed that feeding activity on the *Sargassum* was dominated by three species: the bluespine unicornfish (*Naso unicornis*), the barred rabbitfish (*Siganus doliatus*) and the long-finned drummer (*Kyphosus vaigiensis*; Fig. 5.4). In total, 21,853 bites from nine fish species were recorded on the transplanted *Sargassum* across all treatments and sites, with *N. unicornis*, *S. doliatus* and *K. vaigiensis* accounting for 93.2% of the bites. The remaining six species (*Calotomus carolinus*, *N. brevirostris*, *N. lituratus*, *S. canaliculatus*, *S. corallinus*, and *S. puellus*) accounted for 6.8% of bites and were therefore grouped into 'other' species for subsequent analysis. The overall bite rate (i.e. for all species combined) varied significantly among predator treatments ($F_{3,72} = 101.79$, $P < 0.001$), but not sites ($F_{1,72} = 2.29$, $P = 0.13$) or the interaction of site and predator treatment ($F_{3,72} = 0.78$, $P = 0.51$). The number of bites taken from the *Sargassum* was markedly lower in the presence of the reef shark (3.6 ± 1.7 bites 4.5 h^{-1}) and large coral-grouper (3.2 ± 2.7 bites 4.5 h^{-1}) models than in the presence of the small coral-grouper (181 ± 25.4 bites 4.5 h^{-1}) or in the absence of a predator (905 ± 185.4 bites 4.5 h^{-1}; Fig. 5.4). Given that feeding was negligible on the *Sargassum* in the presence of the large coral-grouper and reef shark models (Fig. 5.4), these treatments were not included in any subsequent analyses.

Comparisons of the feeding rates of the four fish taxa (i.e. *N. unicornis*, *S. doliatus*, *K. vaigiensis* and 'other' species) between the predator absent and small coral-grouper treatments revealed that feeding generally decreased in the presence of the small coral-grouper model, however the differences were not consistent among sites or fish taxa (predator treatment × site: *Pillai's trace* = 0.34, $F_{4,33} = 4.18$, $P = 0.008$; Fig. 5.5). The feeding rate of *N. unicornis* decreased markedly in the presence of the small coral-grouper at the back reef site (from 494.7 ± 154.1 to 6.6 ± 6.4 bites 4.5 h^{-1}), but displayed no change at the lagoon site (Fig. 5.5a; Table 5.1). The feeding rates of *S. doliatus* and 'other' fishes showed significant and consistent declines in the presence of the small coral-grouper (Fig. 5.5b, d; Table 5.1). In contrast, the feeding rate of *K. vaigiensis* differed between sites, but showed no response to the presence of the small coral-grouper (Fig. 5.5c; Table 5.1).

The species richness of herbivorous fishes recorded feeding on the *Sargassum* was greatest in the absence of a predator, and decreased with the presence and size of the predator models (Table 5.2). This pattern was consistent across both sites (Fisher's exact test, $P >$ 0.75). There were also differences in the size frequency distribution of herbivorous fishes observed feeding in the presence of the small coral-grouper and the predator-absent treatment (Kolmogorov-Smirnov lagoon: $D = 0.16$, $P < 0.001$; back reef: $D = 0.59$, $P < 0.001$) with marked reductions in the number of smaller fishes ($\leq$ 25 cm TL) observed feeding in the presence of the small coral-grouper at both sites (Fig. 5.6).

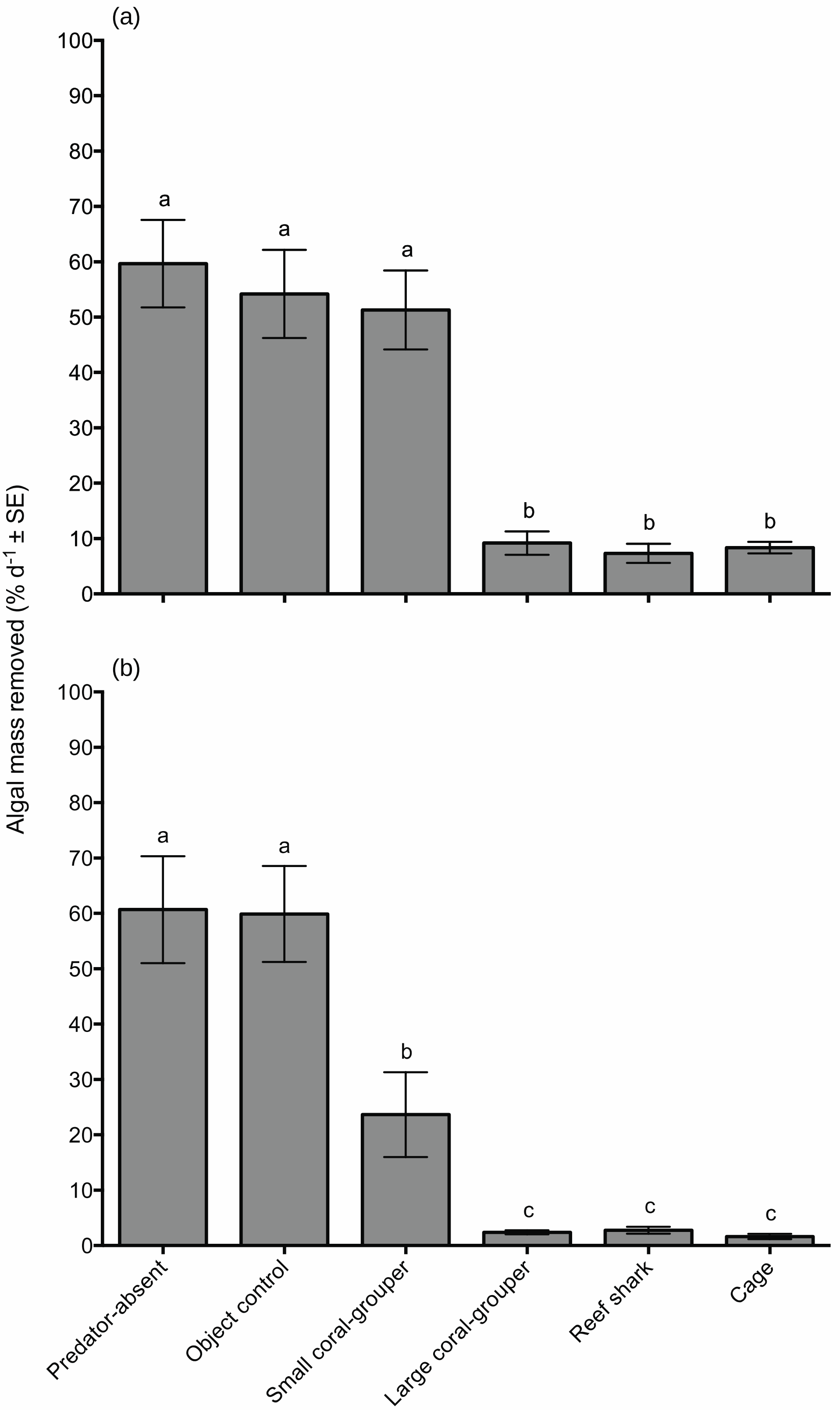

Fig. 5.3. Relative removal rates of *Sargassum* among treatments at (a) lagoon and (b) back reef sites (n = 10). The letters above each bar indicate homogeneous subsets (Tukey's tests).

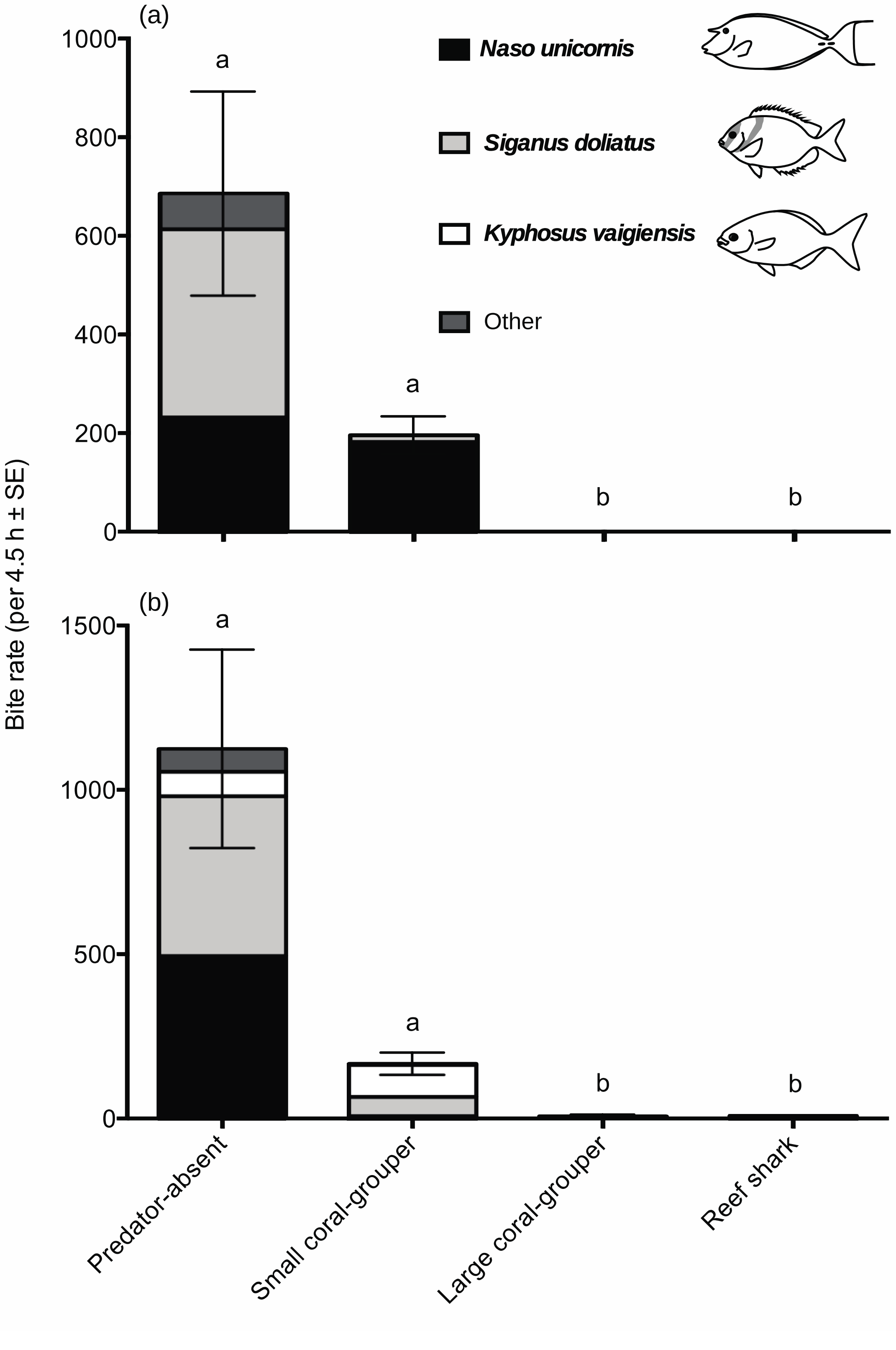

Fig. 5.4. Mean bite rate per 4.5 h treatment time at (a) lagoon and (b) back reef sites. The relative contributions of the three dominant species and other species are shown. Other species include *Calotomus carolinus, Naso brevirostris, N. lituratus, Siganus canaliculatus, S. corallinus* and *S. puellus*. Letters above each bar indicate homogeneous subsets (Tukey's tests). Note differences in scale on y-axis.

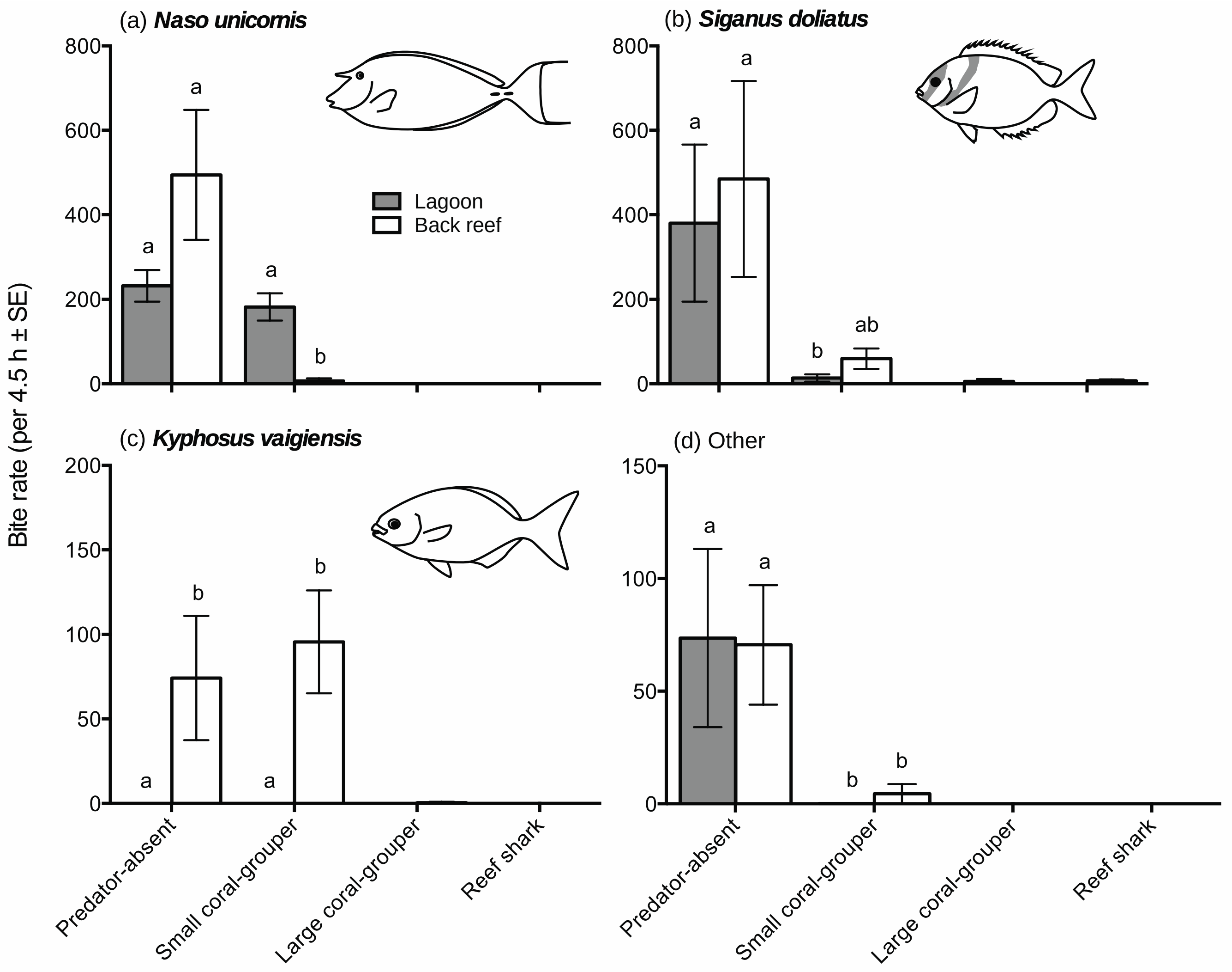

Fig. 5.5. Mean bite rate of (a) *Naso unicornis*, (b) *Siganus doliatus*, (c) *Kyphosus vaigiensis*, and (d) other species, which includes *Calotomus carolinus, N. brevirostris, N. lituratus, S. canaliculatus, S. corallinus* and *S. puellus*. Letters above each bar indicate homogeneous subsets (Tukey's tests). Large coral-grouper and reef shark treatments were not included in analyses (MANOVA) because group means were close to zero. Note differences in scale on y-axis.

Table 5.1. Univariate results from two-factor MANOVA on the effects of site and predator treatment on the bite rate of herbivorous reef fishes contributing to *Sargassum* removal.

Species	Source of variation	d.f.	MS	*F*	*P*
(a) *Naso unicornis*	Site	1	8.833	13.310	< **0.001**
	Treatment	1	10.540	15.882	< **0.001**
	Site x Treatment	1	7.541	11.363	**0.002**
	Error	36	0.664		
(b) *Siganus doliatus*	Site	1	2.273	2.899	0.097
	Treatment	1	14.623	18.650	< **0.001**
	Site x Treatment	1	1.267	1.616	0.212
	Error	36	0.784		
(c) *Kyphosus vaigiensis*	Site	1	13.258	21.276	< **0.001**
	Treatment	1	0.204	0.327	0.571
	Site x Treatment	1	0.204	0.327	0.571
	Error	36	0.623		
(d) Other*	Site	1	0.280	0.615	0.438
	Treatment	1	13.241	29.125	< **0.001**
	Site x Treatment	1	0.002	0.005	0.945
	Error	36	0.455		

Bold indicates a significant difference at a Bonferonni corrected alpha value of 0.0125.

* Other species include; *Calotomus carolinus, Naso brevirostris, Naso lituratus, Siganus canaliculatus, Siganus corallinus, Siganus puellus*.

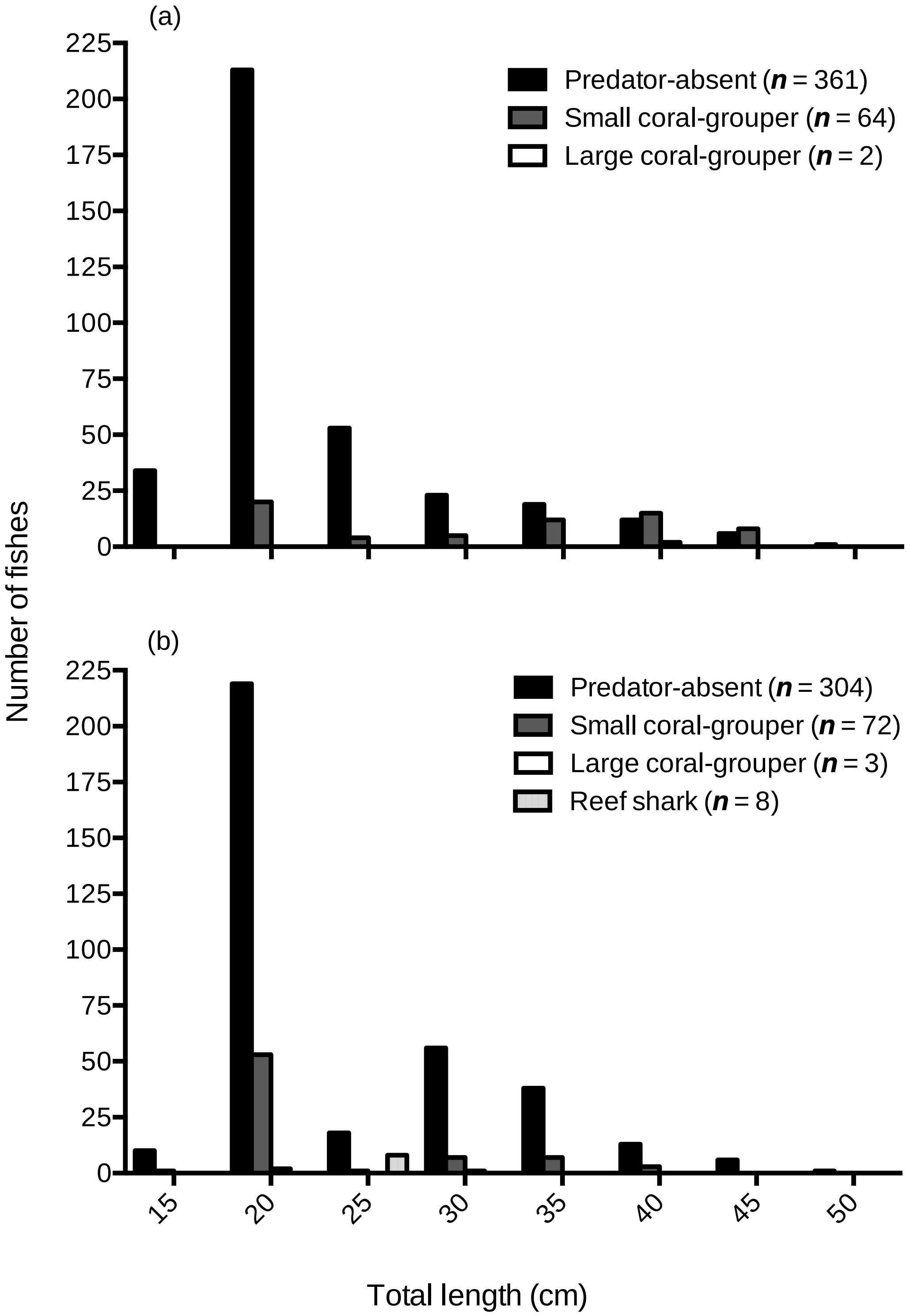

Fig. 5.6. Size frequency distribution of herbivorous reef fishes observed feeding at (a) lagoon and (b) back reef sites. The x-axis labels represent size-class midpoints. Values of *n* are the total number of fishes observed feeding. No values are present for the reef shark treatment at the lagoon site because no individuals were observed feeding. Large coral-grouper and reef shark treatments were not included in analyses (Kolmogorov-Smirnov tests) because group means were close to zero.

Table 5.2. Species of herbivorous reef fishes observed feeding on *Sargassum* at the two study sites.

Site	Treatment	.	*Siganus doliatus*	*Kyphosus vaigiensis*	*Naso brevirostris*	*Naso lituratus*	*Siganus canaliculatus*	*Siganus puellus*	*Siganus corallinus*	*Calotomus carolinus*
(a) Lagoon	Reef shark (*n* = 0)	-	-	-	-	-	-	-	-	-
	Large coral-grouper (*n* = 1)	X	-	-	-	-	-	-	-	-
	Small coral-grouper (*n* = 3)	X	X	-	-	-	-	-	X	-
	Predator-absent (*n* = 7)	X	X	-	X	-	X	X	X	X
(b) Back reef	Reef shark (*n* = 1)	-	X	-	-	-	-	-	-	-
	Large coral-grouper (*n* = 2)	-	X	X	-	-	-	-	-	-
	Small coral-grouper (*n* = 5)	X	X	X	-	-	-	-	X	X
	Predator-absent (*n* = 8)	X	X	X	X	X	-	X	X	X

[*] X indicates that a species was observed feeding.

5.5 Discussion

Apex predators are suggested to play a strong role in indirectly influencing populations of trophic levels that are directly linked to ecosystem functions (Terborgh and Estes 2010), yet there have been few attempts to explicitly demonstrate this in tropical marine systems (see Madin et al. 2010a for exception). Using model predators to simulate predation risk, we found that large predators can have a profound influence on the key ecological process of herbivory on coral reefs, supporting the view that apex predators can influence organisms that are linked to ecosystem functions. In the absence of predators the consumption of macroalgae by herbivores was high (*c*. 60%), but decreased with increasing predation risk. The consumption of macroalgae was reduced by approximately 20% in the presence of the smallest predator (48 cm coral-grouper), and was almost completely suppressed in the presence of the two larger model predators (170 cm blacktip reef shark and 78 cm coral-grouper), presumably due to the perceived risk of predation. Video footage revealed that the overall feeding rate and the number of herbivorous fish species observed feeding on the macroalgae all decreased with increased predation risk. This response to increasing predation risk was most pronounced in smaller (< 25 cm TL) herbivores, with feeding by these fishes declining markedly in response to even the smallest predator. Given the crucial importance of herbivore foraging activity in the functioning of coral reef ecosystems, these results have important implications for our understanding of ecosystem processes and the effects of apex predators on coral reefs

The observed herbivore foraging behaviour and decreased rates of macroalgal consumption near predator models indicate that herbivorous reef fishes display a threat-sensitive response to the presence (or absence) of a potential predator (Helfman 1989). Organisms often make trade-offs between predator avoidance and other fitness-related behaviours (e.g. foraging or reproduction; Lima and Dill 1990), and these trade-offs can vary depending on the risk level posed by the predator. In the present study the consumption of macroalgae and the feeding rate of herbivores both significantly decreased as predation risk increased. While feeding by herbivores was almost completely suppressed in the proximity of the two larger predators, the presence of the smallest predator had a disproportionate effect on the smaller (< 25 cm TL) herbivores. As shallower bodied individuals will be more vulnerable to predation than deeper bodied individuals, this may explain their reluctance to feed near model predators. Together, these results support the supposition that herbivores exhibit threat-sensitive predator avoidance behaviour. Macroalgal removal and bite rate patterns were consistent among all taxa, with the exception of the drummer, *K. vaigiensis*, near the small coral-grouper model; probably because the small coral-grouper does not represent a threat to this robust and deep-bodied species (i.e. the gape limitation of the small coral-grouper meant that it did not represent a predator for all but the smallest *K. vaigiensis*). Notwithstanding, all herbivorous taxa and size classes exhibited the greatest response in the presence of the large coral-grouper and reef shark models. While the presence of static predator models in the present study are likely to have resulted in a redistribution of foraging effort to areas of lower predation risk, as opposed to an overall reduction in foraging rates by herbivores, this behavioural response has potentially important implications for the distribution and biomass of algae on coral reefs. Changes in the densities of predators over larger spatial scales may influence the spatial distribution of herbivore foraging, and/or the overall rates of algal consumption. Further investigations are therefore warranted to assess whether the reaction of herbivores to different densities of mobile apex predators, as opposed to stationary models, integrates up to broad-scale community-level effects.

High algal cover is typically viewed as a sign of degradation on coral reefs, with algae negatively affecting the fecundity, recruitment, and growth of corals (Hughes et al. 2007, Mumby and Steneck 2008). Given that herbivorous fishes play a key role in preventing the proliferation and expansion of algae (Hughes et al. 2007b, Mumby and Steneck 2008), any changes to their behaviour may influence this critical ecosystem process. For example, if predation risk to herbivores alters their activity levels or spatial habitat use this could change the rate at which their impact permeates reef ecosystems. In addition to the changes in foraging of macroalgal consuming (i.e. browsing) fishes in the present study, predator biomass and/or presence has been shown to negatively influence excursion distances of small grazing fishes (i.e. fishes that feed predominately on algal turfs and associated materials) on reefs in the central and western Pacific (Madin et al. 2010a, 2012). Further, several studies have suggested that the 'grazing halos' surrounding structurally complex patch reefs or coral bommies are a result of increased predation risk and hence reduced herbivore feeding with increasing distance from the reef edges (Madin et al. 2011, Downie et al. 2013). Therefore, it appears that behavioural responses to predation risk may be widespread among herbivorous fishes on coral reefs.

Whilst previous studies have highlighted the indirect effects of predators on herbivore behaviour and have linked this to variation in the distribution of algae (Madin et al. 2010a, b, 2011, 2012), the present study is the first to directly quantify the effects of predation risk on algal consumption. Together, these findings demonstrate that changes in foraging behaviour, as a result of the perceived risk of predation, does suppress localized herbivory. These results, however, must be interpreted with prudence. The predator models in this study were stationary, concentrating the risk of predation spatially and thus potentially exaggerating predator effects on herbivore foraging behaviour at the site of the *Sargassum* assay. Indirect effects of mobile predators, such as live reef sharks, are likely to be subtler due to their constant movement. Furthermore, the presence of the predator models in this study represent an acute (short-term) predation risk, and while herbivory was reduced in the presence of the predator models, this localized suppression of herbivory may not necessarily lead to long-term increases in algal biomass within the ecosystem. The perceived risk posed by the predator models may have only led to a redistribution of foraging effort of the herbivorous fishes to areas of lower perceived risk, resulting in heterogenous foraging patterns and patchily distributed macroalgae (Madin et al. 2010b). However if predator densities and the associated predation risk increases over greater spatial and temporal scales, our results may suggest that herbivore foraging effort, and subsequent algal consumption, has the potential to substantially decrease on a community-wide scale. While this prediction is supported by studies in terrestrial systems that have shown significant decreases in foraging effort as a consequence of increased predation risk (see review by Verdolin 2006), it appears to be in contrast to the findings of a study of Caribbean reefs (Mumby et al. 2006). Focused on the direct effects of predation, Mumby and others (2006) demonstrated that a Caribbean marine reserve supported both higher predator biomass (and presumably increased predation risk), higher densities of large-bodied parrotfishes and lower abundance of macroalgae than adjacent fished reefs. It should be noted that parrotfishes are heavily targeted by fishers throughout much of the Caribbean (Rakitin and Kramer 1996), and as such it is difficult to differentiate the positive effects of reduced fishing mortality on parrotfishes from the negative effects of enhanced predation. Further investigation is warranted in order to determine whether these patterns are consistent across ecosystems.

Reefs protected from fishing are typically associated with higher densities of apex predators (Robbins et al. 2006, Nadon et al. 2012, Ruppert et al. 2013) and lower macroalgal cover (Mumby et al. 2006, Sandin et al. 2008, Babcock et al. 2010). As mentioned previously, protected reefs can support higher abundances of both predators and herbivores, because the negative effects of fishing outweigh the negative effects of increased predation, since herbivores become less vulnerable to predation with increasing size (Mumby et al. 2006). The size dependent behavioural effects observed in the present study may therefore provide a mechanism by which herbivores and apex predators can co-exist in relatively high abundances. While low macroalgae cover is typically viewed as a direct result of the higher herbivore biomass on protected reefs, the potential role of predators in influencing algal assemblages through behaviourally-mediated cascades should not be discounted. For example, a recent study on the GBR found that the presence and foraging of both grazing and browsing fishes was negatively related to macroalgal biomass and suggested this was a response to increased predation risk (Hoey and Bellwood 2011). Another study in the central Pacific highlighted that reefs with large predator populations limited the foraging distances of grazing fishes and led to a mosaic of patches of high macroalgal biomass interspersed with closely cropped substrata (Madin et al. 2012). The suppressed rates of macroalgal consumption near predator models provide confidence in our findings that predator presence suppresses localized herbivory, and invariably favours the accumulation of macroalgae biomass on a local scale, however it is unclear whether predation risk will influence algal biomass over larger, reefal scales. Therefore, it is likely that the mechanisms regulating macroalgal growth on coral reefs are more complex than previously understood.

The indirect effects of carnivores on plants mediated by herbivores have been defined as behaviourally-mediated trophic cascades (Dill et al. 2003) and have been documented in numerous ecosystems (e.g. Shurin et al. 2002, Preisser et al. 2005). Here we reveal that apex predators influence herbivore foraging behaviour, which has the potential to drastically influence the amount of macroalgal cover on coral reefs. While our results are consistent with trophic cascade theory, the relatively small spatial scale and the potential reallocation of foraging effort by herbivores calls for caution when interpreting these results. In order to accurately demonstrate a trophic cascade a reduction in herbivory across the entire ecosystem (or reef) would have to be observed. Therefore, while our study provides evidence for a ‘trophic interference’ by apex predators, further studies examining these effects on a larger scale (with contrasting densities of predators) are needed. Trophic cascades involve the influence of both direct and indirect effects of predators, for which there is little data for the tropical marine environment, particularly for large predators. Our study provides the first information on the effects of these large predators and forms a useful basis for future studies.

Evidence from terrestrial systems indicates that apex predators exert a strong influence on other ecosystem components (Estes et al. 2011). However, evidence for behaviourally-mediated or indirect effects of apex predators is rare in the marine realm, particularly on coral reefs. Our findings clearly demonstrate that apex predators can have a strong local influence on a key ecological process on coral reefs; herbivory. Given that apex predators are heavily exploited throughout the world, it is imperative that we better understand both the direct and indirect consequences of their exploitation. Gradients in apex predator density (e.g. inside or outside protected areas) may provide a useful tool in resolving the complexity in the linkages between apex predators, herbivores and algal assemblages.

CHAPTER 6: Reassessing the trophic role of reef sharks as apex predators on coral reefs

Under Revision in *Coral Reefs*

6.1 Synopsis

Apex predators often have strong top-down effects on ecosystem components and are therefore a high priority for conservation and management. However, in high diversity ecosystems such as coral reefs, it is often unclear which species function as apex predators, impeding our ability to manage biological resources at the ecosystem level. Due to their large size and conspicuous predatory behaviour, reef sharks are typically assumed to be apex predators, but this title is tenuous because little is known about their trophic ecology and functional role. In this study, we used stomach contents and stable isotope ratios (δ^{13}Carbon and δ^{15}Nitrogen) to estimate diet, trophic position and sources of primary production for three common species of reef shark (*Triaenodon obesus*, *Carcharhinus melanopterus* and *Carcharhinus amblyrhynchos*) from the Great Barrier Reef (Australia) and evaluated their assumed functional role as apex predators by qualitative and quantitative comparisons with other sharks and large predatory fishes. We found that reef sharks do not occupy the apex of coral reef food chains, but instead have functional roles similar to those of large predatory fishes such as snappers, emperors and groupers, which are typically regarded as high-level mesopredators. We hypothesize that a high degree of functional redundancy exists within this guild of large predators, potentially explaining why shark-induced trophic cascades are rare or subtle in coral reef ecosystems. We also found that reef sharks participate in multiple food webs (pelagic and benthic) and are sustained by multiple sources of primary production, some of which are susceptible to climate-related stressors and may confer vulnerability to reef sharks.

6.2 Introduction

Apex predators such as lions, wolves and orcas occupy the top trophic level of food webs and often have profound top-down effects on prey demography, habitat structure and ecosystem productivity (Estes et al. 2011; Ripple et al. 2014). Accordingly, apex predators are regarded as a key functional group and a high priority for conservation and management (Ritchie and Johnson 2009). However, in some ecosystems, it is unclear which species function as apex predators (Heupel et al. 2014) due to the complexity of food webs (e.g. Bascompte et al. 2005) and intra-specific variation in functional role. For example, coyotes (*Canis latrans*) can function as either apex predators or mesopredators, depending on whether larger carnivores (e.g. wolves) are present (Roemer et al. 2009). Misidentification of apex predators impedes our ability to understand the drivers of community structure, predict the ecological effects of predator removal, and manage resources at the ecosystem level (Heithaus et al. 2008).

Sharks are commonly regarded as apex predators in marine ecosystems (Heithaus et al. 2008; Rizzari et al. 2014a) and their populations are rapidly declining due to the combination of intense fishing pressure and *K*-selected life-history traits (Dulvy et al. 2014; Rizzari et al. 2014b). This is worrisome because altering the density of sharks may invoke community-wide trophic cascades that have far-reaching, detrimental consequences for fisheries resources and the human livelihoods that depend on them (Myers et al. 2007; Heithaus et al. 2008). Therefore, a better understanding of sharks and their trophic functions is imperative for guiding management actions that aim to preserve or enhance ecosystem services.

On coral reefs, sharks can be grouped into two broad categories: (1) true reef sharks, which are most often found on or near coral reefs and tend to be highly conspicuous (e.g. whitetip reef shark, *Triaenodon obesus*; blacktip reef shark, *Carcharhinus melanopterus*;

grey reef shark, *Carcharhinus amblyrhynchos*), and (2) 'other' sharks, which occupy a broad range of habitats, but visit or inhabit coral reefs opportunistically, and tend to be inconspicuous or rare (e.g. tiger shark, *Galeocerdo cuvier*; dusky shark, *Carcharhinus obscurus*; sicklefin lemon shark, *Negaprion acutidens*; tawny nurse shark, *Nebrius ferrugineus*) (Ceccarelli et al. 2014; Heupel et al. 2014). Reef sharks have a strong affinity for reefs with high coral cover and structural complexity (Espinoza et al. 2014; Rizzari et al. 2014c), presumably because these reefs provide the necessary habitat requirements and/or food resources. Knowledge of how reef sharks use these components is important for understanding their vulnerability to global warming and ocean acidification, which are predicted to modify the structure and productivity of coral reefs (Hoegh-Guldberg et al. 2007). Hence, it is critical to identify the sources of primary production that support reef shark populations so we can accurately predict and mitigate the response of reef sharks to environmental change.

Reef sharks are typically assumed to be apex predators (e.g. Friedlander and DeMartini 2002; Sandin et al. 2008; Rizzari et al. 2014a) but this assumption is generally based on their relatively large body size and conspicuous predatory behaviour rather than on detailed knowledge of their diet and trophic ecology. Indeed, anecdotal observations suggest that reef sharks may be more aptly described as mesopredators than apex predators (Mourier et al. 2012; Heupel et al. 2014). If so, then the literature may contain false conclusions regarding trophic structure and food web dynamics of coral reefs (Trebilco et al. 2013; Hussey et al. 2014a; Rizzari et al. 2015), which has important implications for how reef communities are studied and managed. Hence, a comprehensive assessment of the trophic ecology and functional role of reef sharks is warranted.

Several previous studies have examined the diet or trophic position (TP) of reef sharks. The general consensus is that all three species eat mostly teleosts, cephalopods and crustaceans (in decreasing order of importance) and all have a similar TP (~3.7–4.3) (Randall 1977; Stevens 1984; Wetherbee et al. 1997; Cortés 1999; Papastamatiou et al. 2006; Speed et al. 2012). Combined, these results suggest that reef sharks may share a common trophic niche, although there may be a high degree of resource partitioning and geographic separation between species (Kinney et al. 2011; McCauley et al. 2012; Heithaus et al. 2013; Rizzari et al. 2014c). To better understand trophic interactions between reef shark species, and to resolve the enigma surrounding their functional role, more detailed studies of reef shark diet are required, particularly in places where multiple reef shark species co-exist.

The classical approach to trophic ecology has been stomach content analysis (SCA) (e.g. Wetherbee et al. 1997; Papastamatiou et al. 2006), but this method provides only a snap-shot of an individual's diet over a short time period and is biased by a range of factors such as differential rates of digestion (Cortés 1997). To provide a more comprehensive and long-term view of trophic ecology, scientists are increasingly using stable isotope analysis (SIA). This method is based on the concept that stable isotopes such as ^{15}Nitrogen and ^{13}Carbon pass from producers to consumers in predictable quantities, such that the combined measurement of $\delta^{13}C$ (ratio of ^{13}Carbon to ^{12}Carbon) and $\delta^{15}N$ (ratio of ^{15}Nitrogen to ^{14}Nitrogen) in tissue samples provides an integrated food web perspective of diet, TP and sources of primary production (Hussey et al. 2011; McCauley et al. 2012). Despite the advantages of SIA for studying trophic ecology of reef sharks, there have been limited previous attempts to integrate and cross-validate data from SIA and SCA (e.g. Hussey et al. 2011; Vaudo and Heithaus 2011), which limits confidence in studies that utilize only one method.

In this study we used SIA and SCA as complementary methods to investigate the trophic ecology of reef sharks. In particular, we sought to (1) estimate the TP of reef sharks and, by comparison to a guild of mesopredatory reef fishes (snapper, emperor, grouper), assess their assumed status as apex predators, (2) define the trophic niche of reef sharks and thus evaluate the potential for dietary overlap among species, and (3) estimate the contributions of pelagic versus reef-based sources of primary production that support reef shark populations. Integration of this information will provide insights into the functional role of reef sharks and their dependency (or lack thereof) on reef-based primary producers which are forecasted to undergo substantial demographic changes in the near future due to global warming and ocean acidification (Hoegh-Guldberg et al. 2007). Target species were *T. obesus*, *C. melanopterus* and *C. amblyrhynchos*, as these are the dominant reef shark species on Indo-Pacific coral reefs (Ceccarelli et al. 2014; Rizzari et al. 2014c). For purposes of comparison, we also present limited data for some ‘other’ sharks (e.g. *G. cuvier*), but results for this group are only indicative of trends rather than conclusive (due to small sample sizes) so we urge caution when interpreting the data.

6.3 Methods

Study sites and sample collection

The study was conducted in February and June 2013 on coral reefs adjacent to Lizard and One Tree Islands in the northern and southern regions of the Great Barrier Reef (GBR), respectively (Fig. 6.1). To enable capture of the three target shark species, which have slightly different habitat preferences (Ceccarelli et al. 2014; Rizzari et al. 2014c), it was necessary to sample each region at multiple sites (within 5-30 km of each other; Fig. 6.1). Although analysing samples over several sites introduces potential bias due to spatial variation in isotopic signatures of prey and resource pools, any such bias was probably very small (e.g. Heithaus et al. 2013; Shiffman et al. 2014) because the study sites were within the recorded movement distances of reef sharks (Heupel et al. 2010; Whitney et al. 2012; Chin et al. 2013). Furthermore, a multi-site approach allows for detection of robust patterns that transcend small-scale isotopic variations (Heithaus et al. 2013). At all sites, fishing pressure and other anthropogenic influences were low or absent and fauna communities were largely intact, suggesting that trophic interactions and energy pathways were suitably representative of functional coral reefs. For detailed descriptions of the structure and diversity of fish communities on the GBR, see Williams and Hatcher (1983) and Newman et al. (1997).

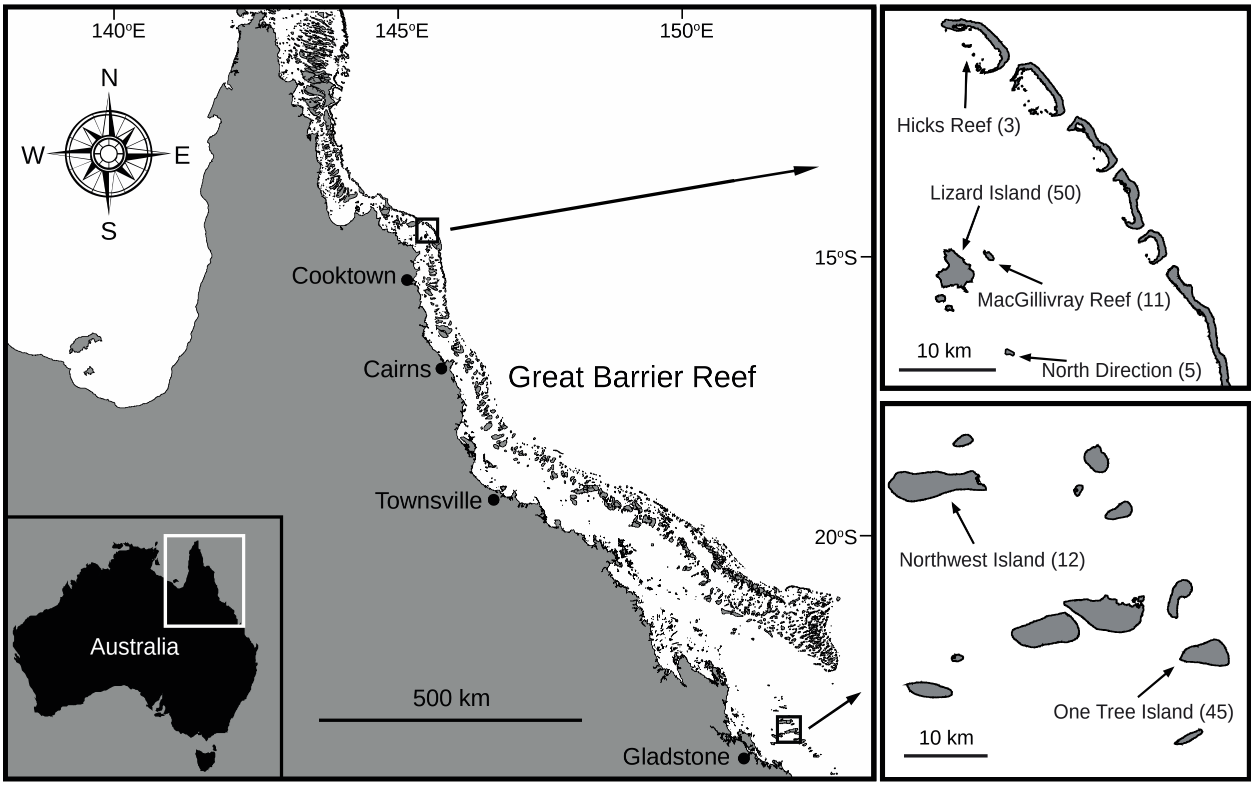

Fig. 6.1. Map showing the location of study sites on the Great Barrier Reef, Australia. Numbers in parentheses depict the sample size for each site (all species combined).

Sharks were captured using a semi-benthic long-line that was positioned 2-5 m above the seafloor on reefs that were 3-25 m deep. The long-line was deployed for periods of 1-1.5 hr between the hours of 0800-1800 and fishing effort was distributed across all major habitat types (i.e. reef slope, lagoon, back reef). The long-line consisted of 10 circle hooks (Mustad, size 14/0) attached to a 50 m rope with 1 m of multistrand wire. Each hook was baited with randomly selected pieces of common reef fishes (scarids, lutjanids, lethrinids, epinephelids, ceasionids and carangids) that were cut into squares to enable differentiation of ingested bait and prey. Upon capture, sharks were restrained on the deck, seawater was applied to the gills, and total length (L_t) was recorded using a flexible tape. Approximately 0.5 cm^3 of white muscle tissue was collected from the anterior dorsal region and then stored frozen (-20 °C) until further analysis. Stomach contents were extracted by gastric lavage, i.e. seawater was pumped into the stomach using an orally-inserted PVC pipe (20 mm diameter). Expelled items were collected in a bucket for later identification in the laboratory. To comply with ethical standards, sharks were released alive and in good condition, except for a subsample of 14 individuals that were dissected to determine the success rate of gastric lavage.

Stable isotope analysis

All samples were oven-dried (60 °C for 48 hr) and grounded to a fine powder using a mortar and pestle. Samples were weighed to the nearest 0.001 g, and isotope content (^{13}C, ^{12}C, ^{15}N, ^{14}N) was measured using a continuous-flow isotope ratio mass spectrometer (Delta V Plus, Thermo Finnigan, Sydney, Australia) coupled with an elemental analyser (ECS 410, Costech Analytical Technologies, Valencia, U.S.A.) at the Advanced Analytical Centre, James Cook University, Australia. Results are expressed as parts per thousand (‰) deviation from Pee Dee Belemnite (vPDB) and atmospheric nitrogen standards for $\delta^{13}C$ and $\delta^{15}N$, respectively. Experimental precision (standard deviation of replicates of internal standard) was 0.1‰ for $\delta^{13}C$ and 0.2‰ for $\delta^{15}N$. All samples had low C:N ratios (mean = 2.94 ± 0.19 standard deviation); therefore it was deemed unnecessary to adjust the data for the potential effects of lipids (as per Post et al. 2007; Hussey et al. 2010; Speed et al. 2012).

The relative influence of region, species, sex and total length on $\delta^{13}C$ and $\delta^{15}N$ were evaluated using boosted regression trees (BRT), which are tree-based models that relate a response variable to multiple predictors using recursive partitioning. For this analysis, tree complexity was restricted to five, learning rate was kept low (0.005), optimal tree number was kept close to 1000, and bag fractions were tested between 0.5 and 0.8 (Elith et al. 2008).

The relative influence of predictor variables was calculated as the percentage reduction in sum-of-squared-error at each iteration and results were validated using ten-fold cross validation (CV) methods (Elith et al. 2008). All BRT models were fitted with R software (R Core Team 2012) using the package *dismo* and additional custom code (Elith et al. 2008). To compare isotopic metrics among species, data were pooled across regions because there were no significant geographic differences in $\delta^{13}C$ and $\delta^{15}N$ signatures (SIBER, $p > 0.15$).

Trophic position (TP) of reef sharks was estimated in two ways. Firstly, TP was estimated assuming constant diet-tissue fractionation, as follows:

$$TP_{constant} = \lambda + (\delta^{15}N_{shark} - \delta^{15}N_{base}) / \Delta_n$$

where λ is the TP of a known base group, $\delta^{15}N_{shark}$ and $\delta^{15}N_{base}$ are the direct estimates of mean $\delta^{15}N$ in each shark species and base group, respectively, and Δ_n is the diet-tissue discrimination factor. The latter was assumed to be constant at 2.3‰ based on the mean fractionation of $\delta^{15}N$ in white muscle tissue of large sharks held in captivity (Hussey et al. 2010). Secondly, TP was estimated using a scaled fractionation approach, as follows:

$$TP_{scaled} = \log_e(\delta^{15}N_{lim} - \delta^{15}N_{base}) - \log_e(\delta^{15}N_{lim} - \delta^{15}N_{shark}) / k + \lambda$$

where $\delta^{15}N_{lim}$ is the saturating isotope limit and k is the average rate at which consumer isotope values approach $\delta^{15}N_{lim}$ per trophic step. $\delta^{15}Nitrogen_{lim}$ and k were assumed to be 21.9‰ and 0.137, respectively, following meta-analysis of experimentally-derived Δ_n in fish (Hussey et al. 2014a,b).

To acknowledge uncertainty in $\delta^{15}N_{base}$, we estimated $TP_{constant}$ and TP_{scaled} using three different base groups; i.e. (1) herbivores (*Siganus doliatus*), (2) small demersal predator (*Thalassoma lunare*), and (3) large pelagic predator (*Scomberomorus commerson*), as reported by Frisch et al. (2014). Base trophic position (λ) of herbivores was assumed to be two, and λ of *T. lunare* (3.65) and *S. commerson* (4.47) were derived from Farmer & Wilson (2011). To calculate mean TP of sharks, each estimate of $TP_{constant}$ was weighted according to λ (rounded down to the nearest integer), because uncertainty increases with each trophic step due to potential error in estimates of diet-tissue fractionation (Hussey et al. 2014a). To calculate mean TP_{scaled}, the arithmetic mean was used.

To evaluate whether reef sharks are apex predators, their TPs and isotopic niches were compared to those of 'other' sharks and large predatory fishes. The latter consisted of leopard coralgrouper (*Plectropomus leopardus*), bar-cheek coralgrouper (*Plectropomus maculatus*), red-throat emperor (*Lethrinus miniatus*) and stripey snapper (*Lutjanus carponotatus*), which are the most abundant, high-level mesopredators on the GBR (Newman et al. 1997; Frisch et al. 2014). All data for predatory fishes originate from the GBR and are reported by Frisch et al. (2014).

Isotope data were plotted in $\delta^{13}C$–$\delta^{15}N$ space and isotopic 'niches' were quantified using Bayesian standard ellipse areas (SEA_B) and small sample size-corrected standard ellipse areas (SEA_C), which were calculated using the SIBER component of the *SIAR* package (Stable Isotope Analysis in R; Jackson et al. 2011). Total size of SEA is a proxy for isotopic trophic diversity within a species, and the extent of overlap of SEA among species indicates the likelihood of interspecific competition for prey (Vaudo and Heithaus 2011).

To estimate the contributions of pelagic versus reef-based sources of primary production that support reef sharks, we used a two-source mixing model with the most ^{13}C-depleted *Scomberomorus commerson* (Spanish mackerel; $\delta^{13}C$ = -17.69) and the most ^{13}C-

enriched *P. maculatus* ($\delta^{13}C = -8.96$) as end members (Frisch et al. 2014). The former is a well-known pelagic piscivore that predominantly eats pelagic fishes such as engraulids and clupeids (Blaber et al. 1990; Farmer and Wilson 2011). The latter is a coral reef piscivore whose distribution is strongly linked to live coral cover (Evans et al. 2010; Frisch et al. 2012).

Stomach content analysis

Stomach contents of reef sharks were identified to the lowest possible taxonomic level. Inter-specific dietary overlap (*D*) was quantified using Schoener's (1968) index, as follows:

$$D = 1 - \tfrac{1}{2}(\Sigma|p_{xi} - p_{yi}|)$$

where p_{xi} and p_{yi} are the relative proportions of prey taxa i for species x and y, respectively. The index ranges from 0 (no overlap) to 1 (complete overlap), and values >0.6 are considered to indicate significant dietary overlap (Schoener 1968). All data are expressed as mean ± standard error (SE) unless otherwise noted.

6.4 Results

Stable isotope analysis

One hundred and twenty-six individuals from three species of reef shark and four species of other shark were analysed for isotopic composition (Table 6.1). The size range of these sharks was very broad (68-158 cm L_t for reef sharks and 95-370 cm L_t for other sharks), although most individuals were of adult size (see Last and Stevens 2009 for sizes at maturity). For reef sharks, the majority of sampled individuals were female (55-73%; Table 6.1), however this had little or no effect on $\delta^{13}C$ and $\delta^{15}N$ isotope ratios (see below).

In general, reef sharks and other sharks were broadly distributed throughout $\delta^{13}C$–$\delta^{15}N$ space (Fig. 6.2), indicating a broad range of trophic diversity. *Triaenodon obesus* had the largest range of $\delta^{13}C$ (6.8‰) and potentially the broadest range of carbon sources, while *C. melanopterus* had the largest range of $\delta^{15}N$ (3.5‰) and potentially feeds over the broadest range of TPs (Table 6.1; Fig. 6.2). Species-specific mean $\delta^{13}C$ values ranged from -14.8 ± 0.7‰ (*G. cuvier*) to -11.4 ± 0.4‰ (*N. acutidens*) and mean $\delta^{15}N$ values ranged from 9.6 ± 0.1‰ (*T. obesus*) to 11.9 ± 0.3‰ (*G. cuvier*), although the single sample of *C. obscurus* measured 13.0‰ (Table 6.1; Fig. 6.2). According to the mixing model, *C. amblyrhynchos* and *G. cuvier* derive the majority (>50%) of their food sources from pelagic-based food webs, which are driven by primary producers such as phytoplankton. In contrast, *T. obesus*, *C. melanopterus*, *N. acutidens* and *N. ferrugineus* derive the majority (>50%) of their food sources from reef-based food webs, which are driven by benthic primary producers such as coral and algae (Table 6.1).

Boosted regression trees (BRTs) indicate that species identity had the highest relative influence on both $\delta^{13}C$ (64.5%) and $\delta^{15}N$ (42.1%), followed by (in decreasing order) L_t ($\delta^{13}C$ = 22.5%; $\delta^{15}N$ = 33.1%), region ($\delta^{13}C$ = 9.1%; $\delta^{15}N$ = 17%) and sex ($\delta^{13}C$ = 3.9%; $\delta^{15}N$ = 7.8%) (Fig. 6.3). Specifically, mean $\delta^{13}C$ was significantly more depleted in *C. amblyrhynchos* than in *C. melanopterus* and *T. obesus* (ANOVA, $F_{2,105} = 38.9$, $p < 0.001$; Tukey's HSD, $p < 0.001$), while $\delta^{15}N$ was significantly more enriched in *C. amblyrhynchos* and *C. melanopterus* than in *T. obesus* (ANOVA, $F_{2,105} = 23.9$, $p < 0.001$; Tukey's HSD, $p < 0.001$; Fig. 6.3a). The total deviance explained by BRT models of $\delta^{13}C$ and $\delta^{15}N$ was 46% and 55% respectively, and the overall predictive performance of BRT models (CV Spearman correlation) was 0.69 ± 0.04 and 0.72 ± 0.08 for $\delta^{13}C$ and $\delta^{15}N$, respectively. Linear regression analysis found no relationship between $\delta^{13}C$ and L_t for any species of reef shark, and only a weak relationship between $\delta^{15}N$ and L_t for *T. obesus* ($r^2 = 0.16$, $F_{1,29} = 2.30$, $p = 0.03$) and *C. melanopterus* ($r^2 = 0.27$, $F_{1,43} = 15.59$, $p < 0.001$), suggesting that size has little influence on TP and no influence on food sources within the range of sizes that we examined (Fig. 6.4). We did not examine relationships between variables in other sharks due to small sample sizes.

Using a constant discrimination factor (2.3‰) and a variety of base groups, mean $TP_{constant}$ of reef sharks (3.8–4.1) was similar to mean $TP_{constant}$ of large predatory fishes (4.0–4.1) but less than mean $TP_{constant}$ of other sharks such as *N. acutidens*, *G. cuvier* and potentially also *C. obscurus* (4.5–5.1) (Table 6.2). Estimates of TP changed little when the scaled approach was used, except that mean TP_{scaled} of *G. cuvier* and *C. obscurus* increased to 5.0 and 5.9 respectively. Note that data for 'other' sharks are only indicative due to small sample sizes and should be interpreted with caution.

Isotopic niches of reef sharks differed in size and position, indicating a moderate to high degree of trophic diversity (Figs 6.5 & 6.6). Ellipse area (SEA_C) was smallest for *C. amblyrhynchos* (1.9 units) and largest for *T. obesus* (3.7 units), with a significant difference between species (SIBER, $p = 0.01$; Table 6.3). Isotopic niche overlap (a proxy for trophic competition) was moderate between *T. obesus* and *C. melanopterus*, minimal between *T. obesus* and *C. amblyrhynchos*, and absent between *C. amblyrhynchos* and *C. melanopterus* (Fig. 6.5; Table 6.3). When considered at the group level, however, there was a high degree of isotopic niche overlap between reef sharks and some species of 'other' sharks and large predatory fishes (Fig. 6.5).

Stomach content analysis

Gastric lavage was demonstrably successful at extracting stomach contents from reef sharks, since only one out of 14 dissected sharks retained any stomach contents after being lavaged, and this particular individual was one of the first to be sampled (i.e. before we perfected the lavage technique). ‘Other’ sharks tended to be much larger than reef sharks, so it was often impossible to restrain (and subsequently lavage) them, which resulted in small sample sizes. Therefore, stomach content data are omitted for ‘other’ sharks.

One hundred and seven reef sharks were subjected to gastric lavage. Stomachs were empty in 42.2, 67.7 and 71.0% of *C. melanopterus*, *T. obesus* and *C. amblyrhynchos* respectively (Table 6.4), and differences between species were statistically significant (X^2_2 = 7.94, p = 0.019). Stomachs in the remaining individuals were found to contain a wide range of prey species, including several species of reef-dwelling herbivores (e.g. parrotfish, surgeonfish, tropical abalone), pelagic planktivores (e.g. hardyheads, fusiliers) and low-level mesopredators (e.g. octopus, wrasse, sea snake), but high-level mesopredators were rare or absent (only one small *L. carponotatus* was found in one stomach of 107 reef sharks). Some prey taxa (e.g. octopus, wrasse, parrotfish) were found in two or more species of reef shark, but the majority of prey taxa were found in only a single species of reef shark (Table 6.5). Mean weight of stomach contents (per shark) was very small (82.1 ± 20.6 g for all reef sharks combined; Table 6.4) and there were no significant differences between species (ANOVA, $F_{2,42}$ = 0.10, p = 0.91). For all three species of reef shark, fish were the dominant prey (64.1%) followed by molluscs (26.5%), and the distribution of major prey types (fish, molluscs and ‘miscellaneous’) was not significantly different between shark species (X^2_4 = 6.84, p = 0.144; Table 6.5). Schoener’s diet overlap index was estimated to be 0.38 (*C. melanopterus* vs *T. obesus*), 0.33 (*C. melanopterus* vs *C. amblyrhynchos*) and 0.44 (*T. obesus* vs *C. amblyrhynchos*), indicating low to moderate levels of dietary overlap.

Table 6.1. Summary of isotopic metrics for reef sharks and 'other' sharks (*)

Species	*n*	Sex ratio (% f:m)	Mean size (L_t ± SE)	Size range (cm L_t)	Mean $\delta^{13}C$ (‰ ± SE)	$\delta^{13}C$ range (‰)	Mean $\delta^{15}N$ (‰ ± SE)	$\delta^{15}N$ range (‰)	Pelagic source[a] (%; mean ± SE)	Reef source[a] (%; mean ± SE)	Ellipse area[b]	Unique area[c] (%)
Triaenodon obesus	31	55:45	125.6 ± 3.4	80 - 151	-12.0 ± 0.3	6.8	9.6 ± 0.1	3.2	34.6 ± 3.3	65.4 ± 3.3	3.7	34.9
Carcharhinus melanopterus	45	73:27	128.0 ± 2.7	68 - 153	-11.4 ± 0.2	4.5	10.4 ± 0.1	3.5	28.2 ± 2.0	71.8 ± 2.0	2.7	38.6
Carcharhinus amblyrhynchos	32	72:28	114.9 ± 5.6	70 - 158	-14.0 ± 0.2	5.2	10.8 ± 0.1	2.2	57.8 ± 2.3	42.2 ± 2.3	1.9	69.3
*Nebrius ferrugineus**	7	86:14	198.0 ± 19.3	121 - 256	-12.7 ± 0.3	2.0	9.9 ± 0.4	2.9	42.7 ± 3.3	57.3 ± 3.3	2.5	15.5
*Negaprion acutidens**	6	33:67	193.0 ± 23.3	95 - 250	-11.4 ± 0.4	2.9	11.2 ± 0.3	1.9	27.7 ± 4.6	72.3 ± 4.6	2.2	67.7
*Galeocerdo cuvier**	4	50:50	241.0 ± 44.8	164 - 370	-14.8 ± 0.7	2.8	11.9 ± 0.3	1.5	67.3 ± 8.1	36.7 ± 8.1	3.3	92.1
*Carcharhinus obscurus**	1	100:0	270.0	-	-13.8	-	13.0	-	55.9	44.1	-	-

[a] End members for the two-source mixing model were the most ^{13}C-depleted *Scomberomorus commerson* (a pelagic specialist) and the least ^{13}C-depleted *Plectropomus maculatus* (a coral reef specialist; data from Frisch et al. 2014).

[b] Ellipse area refers to the corrected standard ellipse area (SEA_C) and is dimensionless.

[c] Unique area refers to non-overlapping ellipse area (see Fig. 6.5; excludes large predatory fishes).

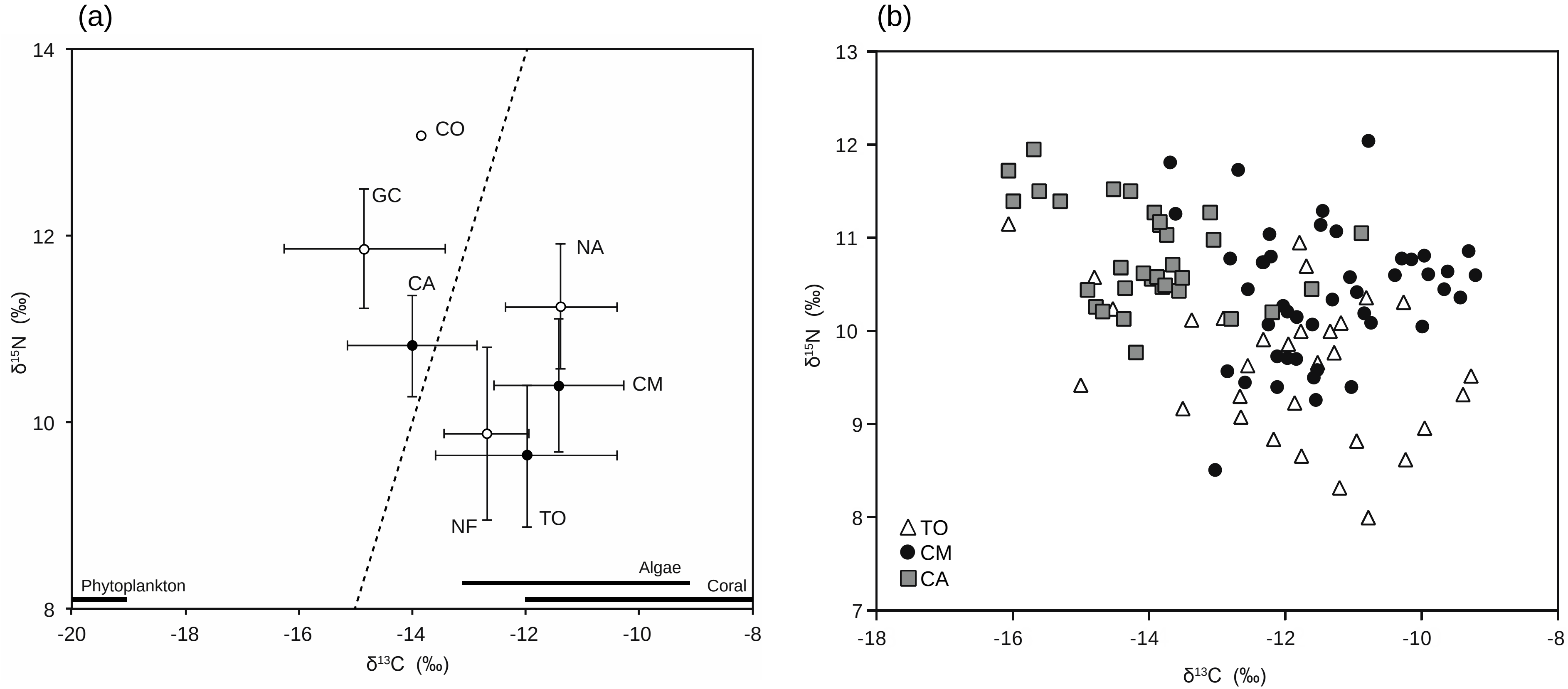

Fig. 6.2. (a) Mean δ^{13}Carbon and δ^{15}Nitrogen (± standard deviation) of reef sharks (TO, CM, CA) and other sharks (NF, NA, GC, CO). White circles indicate species with small sample sizes (n = 1-7), which are shown only for the purpose of comparison. Horizontal lines depict range of δ^{13}C values for common primary producers (see Frisch et al. 2014) and dashed line depicts hypothesised division between pelagic and reef-based food webs (slope of line is approximately 2.3/1.1 due to differential fractionation of δ^{13}Carbon and δ^{15}Nitrogen). (b) δ^{13}Carbon and δ^{15}Nitrogen signatures of individual reef sharks. Abbreviations: TO (*Triaenodon obesus*), CM (*Carcharhinus melanopterus*), CA (*Carcharhinus amblyrhynchos*), NF (*Nebrius ferrugineus*), NA (*Negaprion acutidens*), GC (*Galeocerdo cuvier*), CO (*Carcharhinus obscurus*).

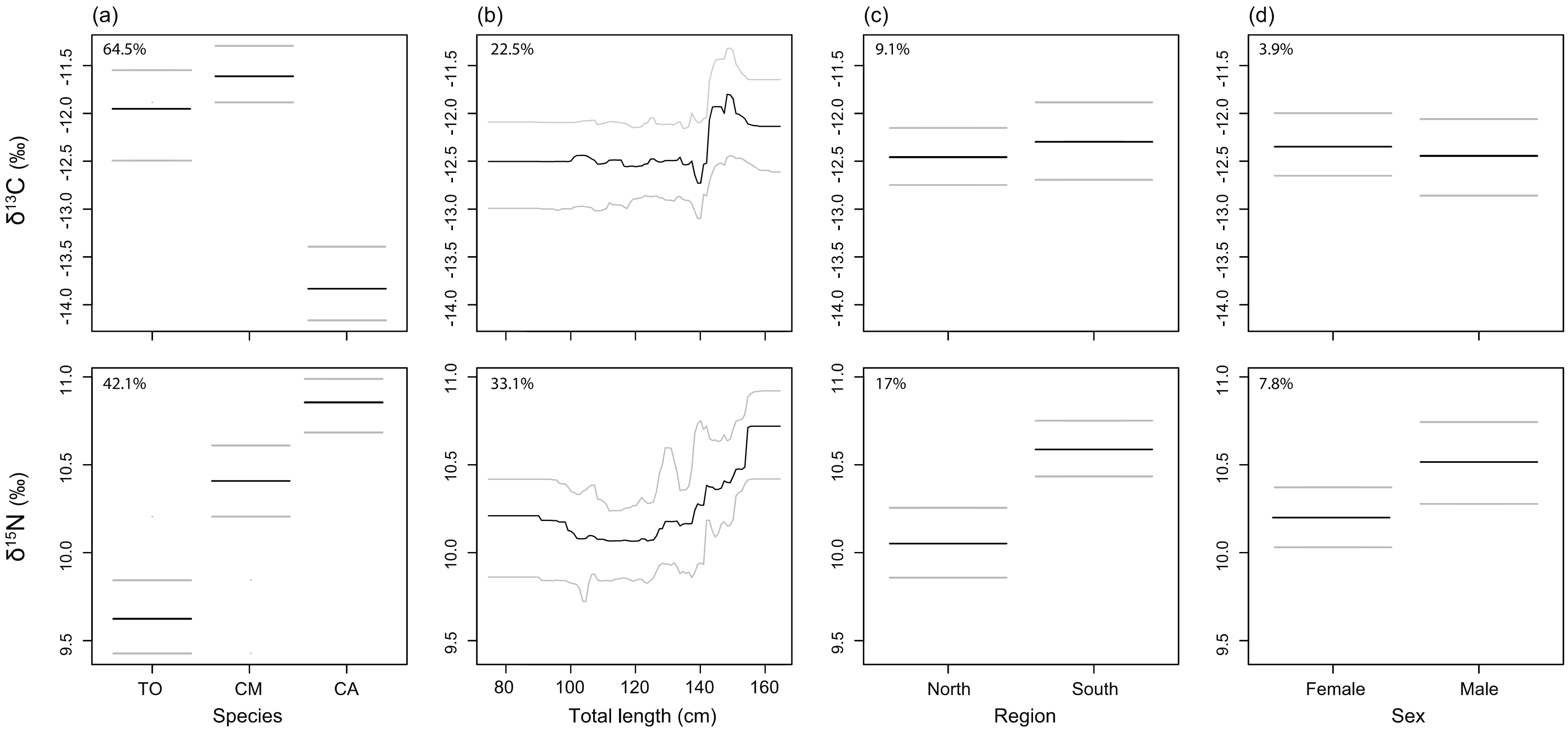

Fig. 6.3. Partial dependence plots of (a) species, (b) total length (cm), (c) region, and (d) sex in boosted regression tree (BRT) models for predicting δ^{13}Carbon (upper panels) and δ^{15}Nitrogen (lower panels). Fitted lines represent the mean estimate (black) and 95% confidence intervals (grey) based on 500 bootstrap replicates. Relative influence (%) of each variable on isotope models is shown in the top left corner of each panel. Abbreviations: TO (*Triaenodon obesus*), CM (*Carcharhinus melanopterus*), CA (*Carcharhinus amblyrhynchos*). Other species are not included due to small sample sizes.

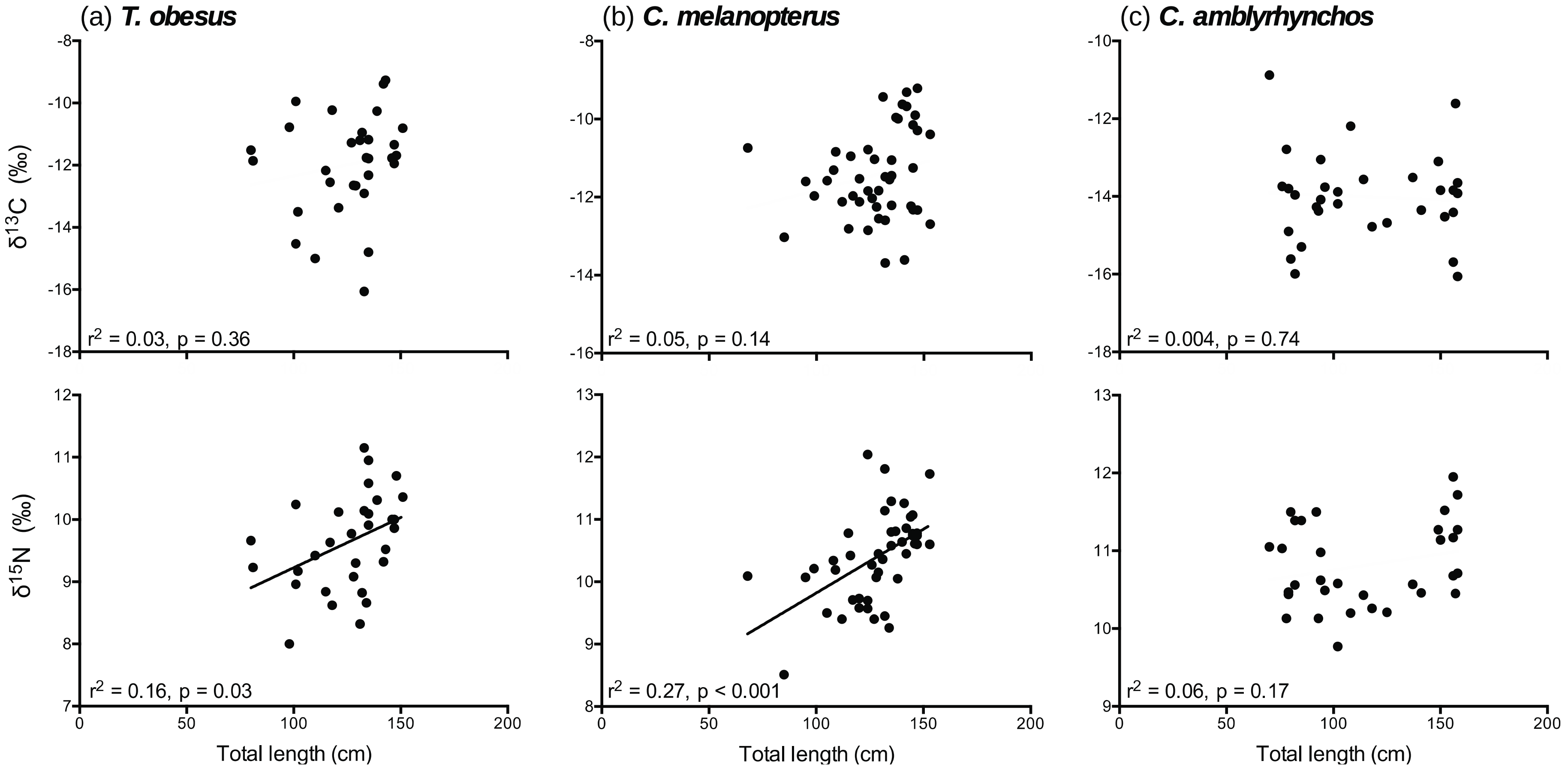

Fig.6.4. Relationship between δ^{13}Carbon (upper panels), δ^{15}Nitrogen (lower panels) and total length in (a) *Triaenodon obesus*, (b) *Carcharhinus melanopterus* and (c) *Carcharhinus amblyrhynchos*. Other species are not included due to small sample sizes. Statistically significant relationships are depicted by regression lines.

Table 6.2. Trophic position (TP) of reef sharks relative to the TP of different base groups, assuming constant and scaled (in parentheses) diet-tissue fractionation (as per Hussey et al. 2010 and Hussey et al. 2014b, respectively). Trophic positions of other sharks (*) and large predatory reef fishes (**) are also shown for comparison (fish data are from Frisch et al. 2014).

Species	Base group[a]			Mean TP (± SE)[b]
	Herbivore ($\lambda = 2$)	Small demersal predator ($\lambda = 3.65$)	Large pelagic predator ($\lambda = 4.47$)	
Triaenodon obesus	3.3 (3.6)	3.8 (3.8)	3.9 (3.1)	3.8 ± 0.1 (3.5 ± 0.2)
Carcharhinus melanopterus	3.6 (4.1)	4.1 (4.3)	4.3 (3.5)	4.1 ± 0.1 (4.0 ± 0.2)
Carcharhinus amblyrhynchos	3.6 (4.3)	4.1 (4.5)	4.3 (3.8)	4.1 ± 0.1 (4.2 ± 0.2)
*Nebrius ferrugineus**	3.3 (3.8)	3.8 (4.0)	4.0 (3.2)	3.8 ± 0.1 (3.6 ± 0.2)
*Negaprion acutidens**	4.0 (4.6)	4.5 (4.8)	4.7 (4.1)	4.5 ± 0.1 (4.5 ± 0.2)
*Galeocerdo cuvier**	4.0 (5.1)	4.5 (5.3)	4.7 (4.5)	4.5 ± 0.1 (5.0 ± 0.2)
*Carcharhinus obscurus**	4.6 (6.0)	5.1 (6.2)	5.3 (5.4)	5.1 ± 0.1 (5.9 ± 0.2)
*Plectropomus leopardus***	3.4 (4.9)	4.2 (5.1)	4.5 (4.4)	4.1 ± 0.3 (4.8 ± 0.2)
*Plectropomus maculatus***	3.4 (4.3)	4.2 (4.5)	4.5 (3.7)	4.1 ± 0.3 (4.1 ± 0.2)
*Lethrinus miniatus***	3.2 (4.6)	4.1 (4.8)	4.4 (4.0)	4.0 ± 0.3 (4.5 ± 0.2)
*Lutjanus carponotatus***	3.3 (4.2)	4.1 (4.4)	4.4 (3.7)	4.0 ± 0.3 (4.1 ± 0.2)

[a] Base δ^{15}Nitrogen values were derived from Frisch et al. (2014) and base trophic positions (λ) were derived from Farmer and Wilson (2011).

[b] Means derived using a constant discrimination factor were weighted according to λ.

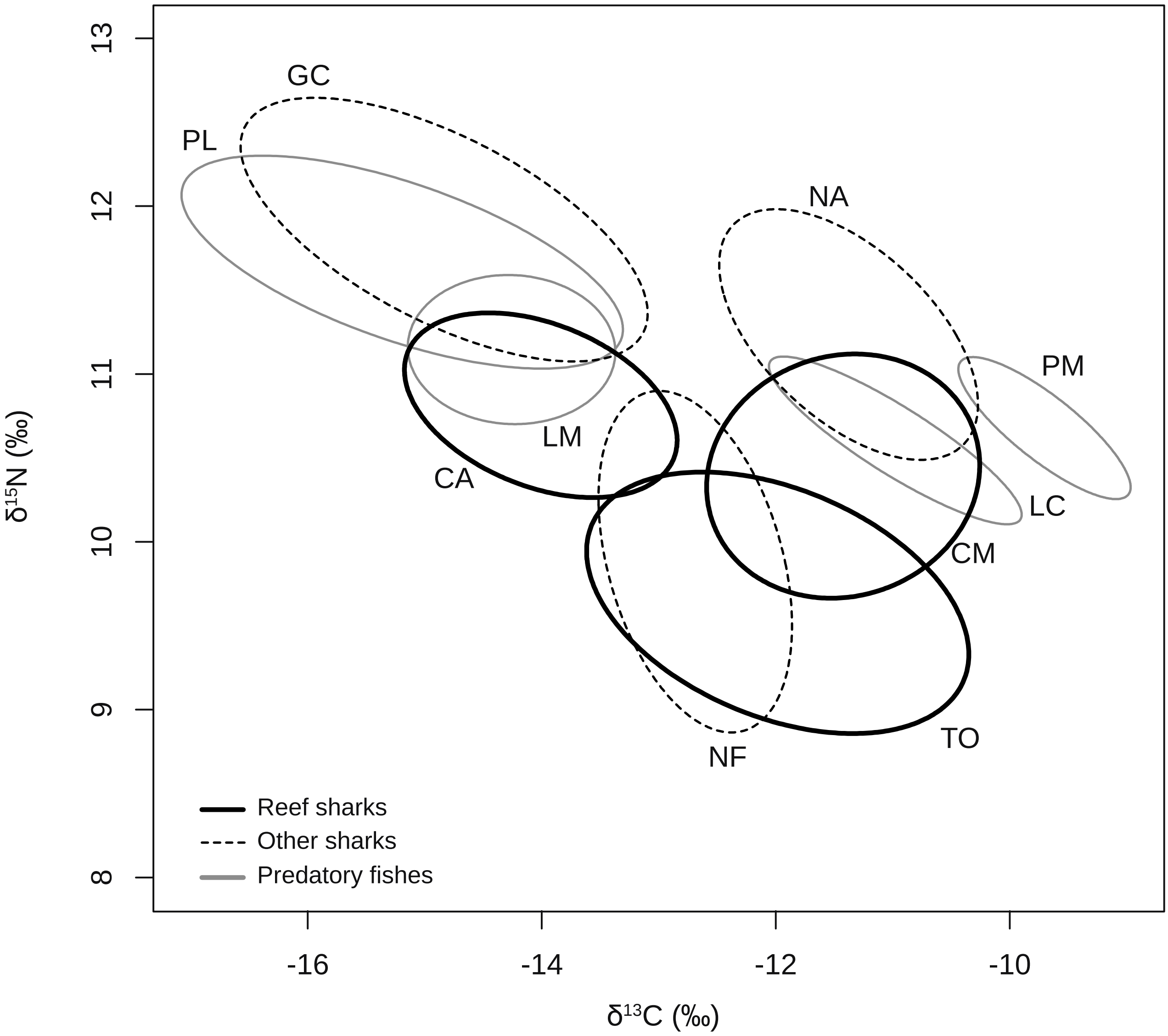

Fig. 6.5. Isotopic niche space of reef sharks, 'other' sharks and large predatory fishes presented as Bayesian ellipses. Note that 'other' sharks had small sample sizes (n = 4-7) and are shown only for the purpose of comparison. *Carcharhinus obscurus* is not included as only a single individual was sampled. Fish data are from Frisch et al. (2014). Abbreviations: TO (*Triaenodon obesus*), CM (*Carcharhinus melanopterus*), CA (*Carcharhinus amblyrhynchos*), NF (*Nebrius ferrugineus*), NA (*Negaprion acutidens*), GC (*Galeocerdo cuvier*), PL (*Plectropomus leopardus*), PM (*Plectropomus maculatus*), LM (*Lethrinus miniatus*), LC (*Lutjanus carponotatus*).

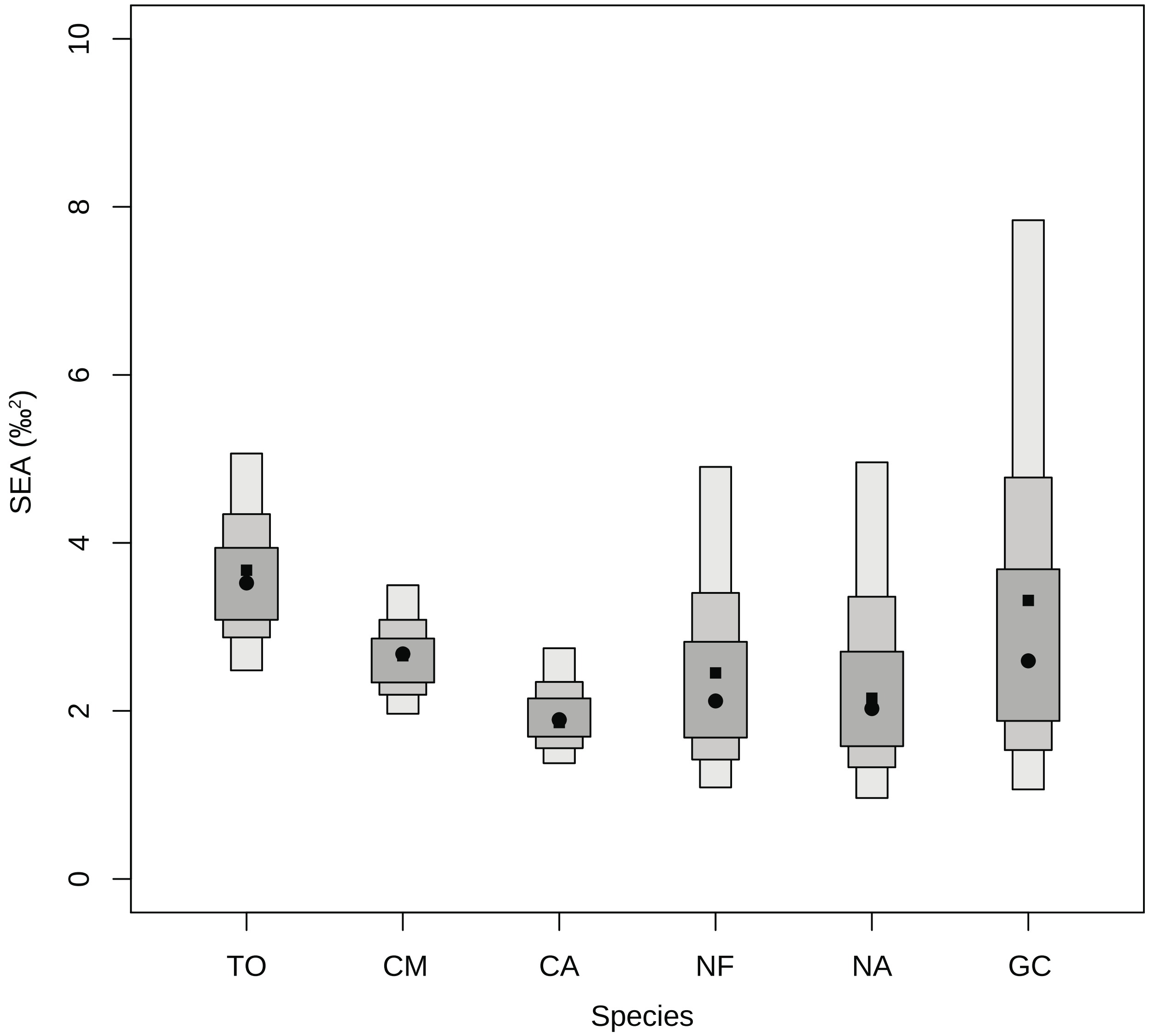

Fig. 6.6. Density plots showing the credibility intervals of Bayesian standard ellipse areas (SEA$_B$). Black circles and squares indicate mode SEA$_B$ and small sample size-corrected SEA (SEA$_C$), respectively. Shaded boxes indicate the 50%, 75% and 95% credibility intervals for each species. Abbreviations: TO (*Triaenodon obesus*), CM (*Carcharhinus melanopterus*), CA (*C. amblyrhynchos*), NF (*Nebrius ferrugineus*), NA (*Negaprion acutidens*), GC (*Galeocerdo cuvier*). *Carcharhinus obscurus* is not included as only a single individual was sampled.

Table 6.3. Interspecific overlap (%) of Bayesian standard ellipse areas (SEA_B) and probability that the SEA_B of one species is larger than the SEA_B of another species (in parentheses). Data should be interpreted as the percentage of SEA_B of Species 1 that is occupied by the SEA_B of Species 2. Bold text indicates a significant difference in SEA_B between two species when $\alpha = 0.05$.

Species 2	Species 1					
	Triaenodon obesus	*Carcharhinus melanopterus*	*Carcharhinus amblyrhynchos*	*Nebrius ferrugineus*	*Negaprion acutidens*	*Galeocerdo cuvier*
Carcharhinus melanopterus	23.56 (0.08)	-	0 (0.90)	14.66 (0.56)	32.34 (0.57)	0 (0.32)
Triaenodon obesus	-	32.58	**0.60** **(0.99)**	73.47 (0.81)	0 (0.81)	0 (0.57)
Carcharhinus amblyrhynchos	0.31	0	-	12.2 (0.27)	0 (0.30)	7.88 (0.14)
Nebrius ferrugineus	49.03	13.53	16.06	-	0 (0.52)	0 (0.32)
Negaprion acutidens	0	26.19	0	0	-	0 (0.31)
Galeocerdo cuvier	0	0	14.03	0	0	-

Table 6.4. Summary of stomach contents of reef sharks. Other sharks are not included due to small sample sizes.

Species	No. of sharks lavaged	% of sharks with empty stomach	No. of sharks with stomach contents	Total no. of prey items	Mean weight of each prey item (g ± SE)	Mean weight of stomach contents (g ± SE)
Triaenodon obesus	31	67.7	10	11	90.0 ± 74.6	99.0 ± 78.3
Carcharhinus melanopterus	45	42.2	26	40	51.4 ± 15.6	79.0 ± 19.3
Carcharhinus amblyrhynchos	31	71.0	9	13	50.0 ± 20.4	72.2 ± 24.5
All reef sharks	107	57.9	45	64	57.7 ± 17.3	82.1 ± 20.6

Table 6.5. Diet composition of reef sharks. Data are expressed as percent frequency of pooled stomach contents. See Table 6.4 for sample sizes. Other sharks are not included due to small sample sizes.

Prey taxa	*Triaenodon obesus*	*Carcharhinus melanopterus*	*Carcharhinus amblyrhynchos*	All reef sharks
Teleost fish (total)	(90.9)	(52.5)	(76.9)	(64.1)
Wrasse (Labridae)	9.1	7.5	0	6.3
Flutemouth (Fistulariidae)	0	7.5	0	4.7
Hardyhead (Atherinidae)	0	5.0	0	3.1
Parrotfish (Scaridae)	27.3	2.5	0	6.3
Eel (Muraenidae)	0	2.5	7.7	3.1
Angelfish (*Centropyge bicolor*)	0	2.5	0	1.6
Snapper (*Lutjanus carponotatus*)	0	2.5	0	1.6
Lizardfish (Synodontidae)	0	2.5	0	1.6
Surgeonfish (*Naso unicornis*)	9.1	0	0	1.6
Fusilier (*Pterocaesio marri*)	9.1	0	0	1.6
Cardinalfish (Apogonidae)	0	0	7.7	1.6
Unidentifiable fish	36.4	20.0	61.5	31.3
Mollusc (total)	(9.1)	(35.0)	(15.5)	(26.5)
Tropical abalone (*Haliotis*)	0	25.0	0	15.6
Octopus (Octopodidae)	9.1	7.5	7.7	7.8
Squid (Loliginidae)	0	2.5	0	1.6
Cuttlefish (Sepiidae)	0	0	7.7	1.6
Other vertebrates (total)	(0)	(7.5)	(7.7)	(6.2)
Sea snake (Hydrophiinae)	0	2.5	7.7	3.1
Bird (Sternidae)	0	5.0	0	3.1
Crustacea				
Crab (Brachyura)	0	2.5	0	1.6
Other				
Coral (Scleractinia)	0	2.5	0	1.6

6.5 Discussion

Analyses of stomach contents and stable isotopes revealed subtle inter-specific differences in the trophic role of reef sharks (*T. obesus*, *C. melanopterus* and *C. amblyrhynchos*), but also a high degree of inter-group trophic overlap between reef sharks, ‘other’ sharks and large predatory fishes. Previously, reef sharks were explicitly or implicitly assumed to be apex predators (Friedlander and DeMartini 2002; Sandin et al. 2008; Rizzari et al. 2014a). However, results from the present study provide three lines of evidence that challenge this assumption. Firstly, δ^{15}N signatures reveal that reef sharks occupy a similar TP to large predatory fishes (putative mesopredators) but a lower TP than other sharks such as *G. cuvier, N. acutidens* and potentially also *C. obscurus* (Table 6.2). Secondly, stomach contents of reef sharks consisted primarily of small fishes (herbivores, planktivores, low-level mesopredators) and molluscs, with few or nil large piscivores (Table 6.5; see also Randall 1977; Stevens 1984; Wetherbee et al. 1997; Papastamatiou et al. 2006). Thirdly, reef sharks and large predatory fishes (e.g. *L. miniatus*, *L. carponotatus*) have broadly similar diets (c.f. Table 6.5; Connell 1998; Kulbicki et al. 2005) and occupy a similar band of isotopic niche space (Fig. 6.5). In addition, reef sharks are known to be eaten by larger sharks such as *G. cuvier* and *Sphyrna mokarran* (great hammerhead shark) (Lowe et al. 1996; Mourier et al. 2012). Collectively, these results provide strong evidence that reef sharks do not occupy the apex of coral reef food chains, but instead occupy trophic niches similar to those of large predatory fishes. These findings have important implications for interpreting the structure and function of coral reef communities and for predicting the effects of predator removal.

Assignment of species into discrete trophic groups (e.g. primary producers, herbivores, apex predators) is standard protocol in ecosystem modelling and has facilitated unique insights into ecosystem function (Trebilco et al. 2013) and alternative management scenarios, which are ultimately used to guide policy decisions (Fulton et al. 2011). In ecosystem models of coral reefs, reef sharks are typically assigned to the apex of food webs (e.g. Bozec et al. 2004; Bascompte et al. 2005), but our results indicate that this practise misrepresents trophic structure among high TP species and potentially distorts model outputs. Hence, we advocate a reassignment of reef sharks to an alternative trophic group (e.g. high-level mesopredators) that better reflects trophic similarities between reef sharks and large predatory fishes. This change is expected to increase the accuracy of ecosystem models, refine our understanding of how reef communities function, and, ultimately, improve management of reef sharks.

Removal of apex predators such as wolves, lions and dingoes can invoke trophic cascades due to release of numerous prey species and subsequent flow-on effects to lower trophic levels (Estes et al. 2011; Ripple et al. 2014). However, trophic cascades induced solely by removal of reef sharks are rare, subtle and/or equivocal (Heithaus et al. 2010; Ruppert et al. 2013; Rizzari et al. 2015), implying that reef sharks have relatively weak effects on community structure and function (see also Heupel et al. 2014). A potential explanation is that functional redundancy exists among large piscivores, such that equivalent species (e.g. large predatory fishes) compensate for any loss of reef sharks and thus buffer potential trophic cascades. This hypothesis is supported by results from the present study, which indicate that (1) reef sharks and large predatory fishes are functionally similar (based on equivalent mean TPs and overlapping isotopic niches; Tables 6.2 & 6.3), and (2) these two groups of predators are dietary generalists (Table 6.5; Connell 1998; Kulbicki et al. 2005) and potentially consume prey in proportion to availability (Kingsford 1992), thereby compensating for loss of species-level interactions. It is also noteworthy that large predatory reef fishes are highly diverse (>20 species on the GBR) and probably encompass a broader range of trophic niches than those of the four species considered here. In view of these results, we contend that functional redundancy exists among large piscivores and is sufficiently high on the GBR to stabilize community structure despite moderate to high fishing pressure and depletion of reef sharks in some areas (Rizzari et al. 2015).

Bivariate isotope data (Fig. 6.2) and stomach contents (Table 6.5) indicate subtle inter-specific differences in diet and low to moderate inter-specific competition for prey among reef shark species. Limited or incomplete trophic overlap is thought be a prerequisite for competitor coexistence and has been previously documented within predatory communities of a broad range of animal taxa (Woodward and Hildrew 2002; Heyward and Kerley 2008), but only rarely in predatory communities where species show strong morphological, taxonomic and habitat similarities (Heithaus et al. 2013; Kiszka et al. 2014). With regard to trophic diversity, total area of isotopic niche space was substantially larger for *T. obesus* than for *C. melanopterus* and *C. amblyrhynchos* (Table 6.1), indicating that *T. obesus* is more generalist (less specialist) in its diet and is perhaps more resilient to environmental disturbances that alter the composition of reef fish communities.

Mean δ^{13}C (an indicator of food source) of reef sharks indicates that they participate in multiple food webs and are sustained by multiple sources of primary production. According to the mixing model, *C. amblyrhynchos* derive the majority (58%) of their carbon from pelagic sources such as phytoplankton, whereas *T. obesus* and *C. melanopterus* derive the majority (65% and 72%, respectively) of their carbon from benthic reef-based sources such as coral (Table 6.1; see also McCauley et al. 2012). Due to the effects of global warming and ocean acidification, the abundance of corals and coral-dependent fishes is expected to decline during the next century (Hoegh-Guldberg et al. 2007), with unknown but potentially severe consequences for reef sharks. Vulnerability to these climate-related stressors is predicted to be highest for *C. melanopterus* and lowest for *C. amblyrhynchos* due to differential utilization of benthic reef-based sources of production. Therefore, species-specific conservation action may be warranted to offset disparate climate-associated risks to each reef shark species.

The traditional view of coral reefs is that benthos such as coral and algae are the ultimate sources of carbon available to reef-associated consumers (Polunin 1996; Bozec et al. 2004). However, it is now evident that planktonic producers are also an important source of carbon for reef sharks, particularly *C. amblyrhynchos* (Table 6.1; see also McCauley et al. 2012). Protection of pelagic habitats is therefore an important component of reef shark conservation and lends support for an integrated or ecosystem-based approach to management of coral reefs. Despite the importance of pelagic prey to *C. amblyrhynchos* (inferred from Table 6.1; see also McCauley et al. 2012), surprisingly few were identified in stomach contents (Table 6.5; see also Wetherbee et al. 1997; Papastamatiou et al. 2006). Although it is possible that *C. amblyrhynchos* regurgitated much of their stomach contents during capture on the long-line (see below), a more likely explanation is that SCA under-estimated the consumption of pelagic prey, potentially because common pelagic fishes such as clupeids and engraulids are small, soft-skinned and thus rapidly digested (relative to coral reef prey). Differential digestion is a fundamental problem with SCA (Cortés 1997) and highlights the utility of stable isotope analyses as a complimentary method for investigation of trophic ecology.

It is noteworthy that herbivores such as parrotfish and unicorn surgeonfish (*Naso unicornis*) were found in the stomachs of *T. obesus* (Table 6.5; see also Randall 1977) and that both predator and prey have closely matching δ^{13}C signatures (c.f. Table 6.1; Frisch et al. 2014). Reef-based herbivorous fishes, particularly *N. unicornis*, have keystone characteristics and are thought to be critical for maintaining the competitive balance between corals and algae (Hoey and Bellwood 2009). Due to direct (consumptive) and indirect (behavioural) effects of reef sharks on herbivorous fishes, a primary concern is that reef sharks may suppress recovery of degraded coral reefs (Rizzari et al. 2014a). However, reef shark prey are typically small (Table 6.4), so it is likely that herbivorous fishes achieve a size refuge and escape the risk of predation at a relatively early age (Mumby et al. 2006). Build-up of reef sharks in marine reserves is therefore unlikely to pose a threat to net grazing capacity of herbivorous fishes or overall health of coral reefs.

The interpretations and predictions presented thus far are dependent on two key assumptions. Firstly, it was assumed that the reef- and pelagic-based sources of production that we represented with end members in the mixing model were the key sources of production that sustain reef sharks (i.e. these consumers primarily rely on some combination of reef and pelagic production) and not on additional or alternate sources such as deep-water inter-reef food webs. Although the selected end members almost certainly do not represent the complete isotopic signature of reef and pelagic food webs, concordance between the isotopic signatures of end members and relevant producers (Frisch et al. 2014) suggests that the selected end members do indeed serve as suitably accurate isotopic proxies for reef and pelagic systems. Secondly, it was assumed that the high proportion (42.2–71.0%) of reef sharks with empty stomachs was not caused by regurgitation during capture on the long-line. This assumption is supported by three lines of evidence: (1) a high proportion of diver-speared reef sharks have empty stomachs (authors' pers. obs.), (2) nil reef sharks were seen to regurgitate voluntarily, either in the water or on deck, and (3) some reef shark stomachs contained square-cut pieces of bait, indicating that recently ingested food was not regurgitated. Although a high proportion of empty stomachs is common in reef sharks (Randall 1997; Stevens 1984; Wetherbee et al. 1997), this phenomenon limits the utility of SCA due to the need for large sample sizes. However, the strong and consistent congruence of results obtained by SCA and SIA in this study confirms the validity of carbon and nitrogen isotopes as accurate and robust proxies for diet and associated trophic metrics of reef sharks.

In summary, the combined application of SIA and SCA has revealed new paradigms with respect to trophic ecology of reef sharks. In particular, it is apparent that reef sharks do not occupy the apex of coral reef food chains, but instead have functional roles similar to those of large predatory fishes such as snappers, emperors and groupers, which are typically regarded as high-level mesopredators. Hence, there is probably a high degree of functional redundancy in this guild of large predators, potentially explaining why shark-induced trophic cascades are rare or subtle on coral reefs. It is also apparent that reef sharks participate in multiple food webs and are sustained by multiple sources of primary production, some of which are susceptible to climate-related stressors and may confer vulnerability to reef sharks. In conclusion, we assert that large conspicuous predators, be they elasmobranchs or any other taxon, should not axiomatically be regarded as apex predators without thorough analysis of their diet. In the case of reef sharks, which were previously assumed to be apex predators, our dietary analyses suggests they should be reassigned to an alternative trophic group such as high-level mesopredators. This change will increase accuracy of ecosystem models, providing resource managers with improved tools for understanding how reef communities function and how removal of predators (e.g. via fishing) might affect ecosystem properties. These improvements are imperative and urgent given the recent declines in reef shark populations (see Rizzari et al. 2014b and references therein) and the intensifying threats they will face in the future.

CHAPTER 7: General Discussion

Trophic interactions fundamentally shape ecosystem structure and impart stability, ultimately regulating productivity and ecosystem services that, in some cases, benefit humans. Knowledge of these trophic interactions, and the species involved, are central to our understanding of the processes that structure ecological systems. Furthermore, understanding trophic interactions can provide scientists and resource managers with a framework to model disturbance effects such as human impacts on community structure (Pinnegar et al. 2002; Dulvy et al. 2004), altered trophic linkages (Pauly et al. 1998), and effects of species removals (Stevens et al. 2000). An increasingly important aspect of trophic ecology is to understand the roles of large predators (Segio et al. 2014), as it has recently been argued that the loss of this guild is the most pervasive impact of humankind on the natural world (Estes et al. 2011). However, empirically defining the role of large predators in mediating species interactions, and the strength of those interactions, still remains a major challenge for ecosystem ecology (Rooney et al. 2008).

In five related studies, this thesis revealed important new insights relating to the biology and assessment of reef sharks. In Chapter 2, an evaluation of five different survey methods (timed-swims, towed-diver, baited-remote-underwater-video, stationary-point-count, and audible-stationary-count) found that diver-based visual transects were minimally influenced by shark behavior towards humans, regardless of opportunities for prior interactions. Application of this survey method on the Great Barrier Reef, the world's largest reef, revealed that the highest densities of reef sharks occur on the reef slope with high levels of coral cover and structural complexity (Chapter 3), and in management zones where humans are excluded (Chapter 2; see also Robbins et al. 2006). Despite a strong gradient in reef shark density, there was substantial variation in the behavioural and numerical responses of lower trophic level organisms (Chapters 4 and 5). This variation is hypothesised to be the result of a high degree of functional redundancy of reef sharks with other large predatory teleost fishes (Chapter 6), which may explain why shark-induced trophic cascades are rare (Ruppert et al. 2013) or non-existent (Rizzari et al. 2015) on coral reefs.

Building on a growing body of literature aimed at identifying the influence of large predators on lower trophic levels, particularly herbivores (Heithaus et al. 2008; 2014), this thesis reveals that large predator effects can be variable on coral reefs. Numerous studies conducted on coral reefs have reported behavioural changes of herbivores in response to predator presence (Madin et al. 2010a,b, 2011, 2012). However, none of these studies have assessed whether these behavioural alterations manifest to changes in algal consumption and ultimately algal biomass. Given the importance of herbivores to coral reef ecosystem function (Hughes et al. 2007b; Rasher et al. 2013), it is important that scientists and mangers know the potential flow-on effects of large predators to algae consumption by herbivores. Examining this process via a manipulative field experiment, this thesis demonstrates that algal consumption by herbivores is substantially reduced due to the perceived risk of predation (Chapter 5), extending the findings of previous research (Madin et al. 1010a,b). Thus, it appears that large predators can potentially indirectly influence the distribution of algae on coral reefs, which is an important consideration for ecosystem models. However, further work is needed to validate the plausibility of a trophic cascade beause the evidence only shows a spatial displacement of herbivores, but no specific evidence of a decrease in total consumption rate of algae.

Despite evidence supporting the notion that reef sharks can potentially elicit a trophic cascade on coral reefs (Chapter 5), this finding appears to only hold true on a localized context. When examining the influence of reef sharks on lower trophic levels at a larger spatial scale, no correlative trophic link was found between predators and herbivores

(Chapter 4). Recent studies examining the ecological role of reef sharks and their influence on community structure have generated inconsistent conclusions (Friedlander and DeMartini 2002; Sandin et al. 2008; Houk and Musburger 2013; Ruppet et al. 2013; Rizzari et al. 2015). The removal of reef sharks via fishing is often hypothesised to invoke trophic cascades due to release of numerous prey species and subsequent flow-on effects to lower trophic levels (Bascompte et al. 2005; Estes et al. 2011). However, trophic cascades induced solely by removal of reef sharks are rare, subtle and/or equivocal (Heithaus et al. 2010; Ruppert et al. 2013; Chapter 4), implying that reef sharks have relatively weak effects on community structure and function. A potential explanation is that functional redundancy exists among large piscivores (Chapter 6), such that equivalent species (e.g. large predatory fishes) compensate for any loss of reef sharks and thus buffer potential trophic cascades.

Reef sharks are typically assumed to be apex predators (e.g. Friedlander and DeMartini 2002; Sandin et al. 2008; Rizzari et al. 2014a), and are therefore expected to influence community structure similarly to other apex predators (e.g. Heithaus et al. 2008; Estes et al. 2011). However, this assumption is generally based on reef sharks' relatively large body size and conspicuous predatory behaviour rather than on detailed knowledge of their diet and trophic ecology. Anecdotal observations even suggest that reef sharks may be more aptly described as mesopredators than apex predators (Mourier et al. 2012; Heupel et al. 2014). If so, then the literature may contain misleading conclusions regarding trophic structure and food web dynamics of coral reefs (Trebilco et al. 2013; Hussey et al. 2014a; Rizzari et al. 2015). This thesis provides one of the first detailed investigations of reef shark diet, incorporating both stomach contents and stable isotopes, the results of which provide multiple lines of evidence challenging the assumption that reef sharks are apex predators. Firstly, the trophic position of reef sharks strongly overlapped with those of other predatory fishes, but was lower than other sharks, such as tiger sharks (Frisch et al. 2014; Chapter 6).

Secondly, stomach contents of reef sharks revealed that they feed primarily on small teleost fishes and molluscs, with few (or nil) large piscivores. Thirdly, reef sharks and other predatory fishes occupy a similar band of isotopic niche space and reef sharks are known to be eaten by larger sharks (e.g. hammerhead and tiger sharks; Lowe et al. 1996; Mourier et al. 2012). Lastly, stomach contents revealed that reef sharks exhibit diffuse predation (Menge et al. 1994) – that is where a suite of species all prey on a wide portfolio of shared prey resources, such that individual predator species have little measurable effect (i.e. high redundancy). Diffuse predation is a common characteristic of mesopredators rather than apex predators that exhibit concentrated predation (i.e. one predator species determines patterns of community structure, such as the behaviour, distribution, composition and diversity of prey; Menge et al. 1994). Combined, these results suggest that large conspicuous predators in any given ecosystem should not axiomatically be regarded as apex predators. In the case of reef sharks, this thesis provides support for reassigning them to an alternative trophic group such as high-level mesopredators. This change will have important implications for interpreting their role in structuring reef communities and improving the accuracy of ecosystem models, thus providing management with improved tools for understanding how the removal of predators (e.g. via fishing) influences ecosystem properties.

A topic of recent interest is the role of larger, transient shark species (e.g. tiger, bull, silvertip and hammerhead sharks) as apex predators on coral reefs. The results of this thesis provide empirical support for the initial claims made by Heupel et al. (2014) that larger, transient sharks are in fact the true apex predators on coral reefs, whereas reef sharks are more likely to function as mesopredators. This is supported by the results of tiger shark and dusky whaler shark trophic positions compared to reef sharks (Chapter 6). However, given the small number of samples collected from these species further work is needed to validate this hypothesis in order to determine the role and extent that larger, more mobile sharks play in structuring coral reef food webs.

Collectively, the results of this thesis highlight that top-down forcing by reef sharks on coral reefs is variable and may not play as strong a role as previously thought and that current management regimes addressing only top-down forces may inadequately protect ecosystem function. A sound understanding of trophic interactions underpins our ability to accurately predict ecosystem responses to change. It appears that traditional trophic theories adopted from terrestrial realms are not applicable to all ecosystems; thus, the findings of this thesis add credence to the call for a restructuring of marine food webs (Trebilco et al. 2013; Hussey et al. 2014a).

Future directions

The traditional framework and theory proposed to examine the interactions and structure of marine food webs is largely adapted from the terrestrial realm, whereby species' roles are categorised or compartmentalised into simplified functional groups or trophic levels (TL) and are limited to four levels (TL 1 = primary producers, TL 2= herbivores, TL 3 = mesopredators, TL >4 = apex predators). For terrestrial ecosystems, top predators are mostly mammals or birds that have long periods of dependency (i.e. post-birth parental care) and adopt a diet very similar to adults from a young age (e.g. highlighted by Heupel et al. 2014). However, in the marine realm, fishes can grow through up to six orders of magnitude during their lives, leading to ontogenetic variations in diet due to increasing gape size and the ability to feed on increasingly large prey (Scharf et al. 2000). Ontogenetic variations in diet, however, are not equal across species. Higher trophic level organisms, such as large predators, exhibit greater shifts in diet than lower trophic groups such as herbivores, which typically feed on the same resource (e.g. algae) or a limited number of resources irrespective of their size or life-stage (e.g. Bellwood 1988). This suggests that mean trophic level and interaction strengths are strongly size-dependent (Jennings et al. 2008; Trebilco et al. 2013), rather than species-dependent, which forms the basis of traditional functional ecology and guild theory. Consequently, marine communities can be viewed as size-structured, with organisms generally feeding on prey smaller than themselves (Barnes et al. 2010).

Further impeding our ability to accurately understand trophic interactions is that the structure of food webs is commonly built on the assumption that species interactions are static, with each species having a 'fixed' role. This assumption has arisen because we typically only look at the structure of the food webs at one time point (i.e. interactions are held constant over time and space). This generalised approach has formed the basis of most traditional ecosystem studies and resource management modelling (e.g. Mumby et al. 2007; Sanders et al. 2013; including some of the results from this thesis), but has ultimately led to over-simplification (highlighted by Hussey et al. 2014a). Within this static framework, it is automatically assumed that variations in spatio-temporal flexibility between, or within, trophic levels are non-existent. However, the proportion of time that a predator spends within an ecosystem or the amount of overlap between a predator's home range and a discrete ecosystem can vary substantially (e.g. Matich et al 2011), with associated impacts on lower trophic species that are often more resident within that system. For example, on coral reefs, resident blacktip reef sharks derive the majority of their diet from the fore-reef environment (McCauley et al. 2012; Chapter 6), while tiger sharks may only be resident and feed on a reef for a period of days before undertaking large-scale movements to distant reef systems (Werry et al. 2014). Despite marked differences in movement behaviours, these and other shark species are typically grouped into the same trophic guild of apex predators (e.g. Friedlander and DeMartini 2002). This inherently assumes that all sharks play a similar functional role in reef ecosystems. Ignoring variation in the extent of movements or home range overlap with a given ecosystem or across multiple ecosystems precludes our ability to accurately depict trophic interactions within those systems, which has consequences for the accuracy of static frameworks that are used to inform management. Therefore, future work should aim to incorporate variability in shark movement into trophic modeling in order to produce a more accurate representation of species interactions.

In order to gain a better understanding of trophic interactions, and develop an accurate framework for predicting impacts of disturbance events (e.g. species removals) on ecosystem structure, it is important to understand and incorporate the plasticity of trophic interactions into marine food webs. This can be accomplished by accounting for animal movement in mediating trophic interactions on a size-based, rather than species-based framework (e.g. Hertz et al. 2014; Kiszka et al. 2015; Matich and Heithaus 2015). Incorporating such information will provide a more robust approach to elucidate food web structure and represent trophic interactions more accurately than traditional static food webs.

Conclusions

In conclusion, this thesis has advanced our understanding of reef sharks, particularly in terms of their response to protection from fishing, spatial distribution, behaviour towards divers, and their functional roles on coral reefs. Avenues of future research that will be fruitful for further understanding food web structure and stability on coral reefs are also highlighted. These advances will be important for improving ecosystem-based management strategies that aim to conserve not only individual species, but also their functions and interactions. Such an approach is paramount given that coral reefs around the world face intensifying anthropogenic threats such as overfishing and climate change.

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APPENDIX A: Author's publication list

Publications arising from this thesis

Rizzari JR, Frisch AJ, Connolly SR (2014) How robust are estimates of coral reef shark depletion? Biological Conservation 176: 39-47

Rizzari JR, Frisch AJ, Magnenat KA (2014) Diversity, abundance, and distribution of reef sharks on outer-shelf reefs of the Great Barrier Reef, Australia. Marine Biology 161: 2847-2855

Rizzari JR, Frisch AJ, Hoey AS, McCormick MI (2014) Not worth the risk: apex predators suppress herbivory on coral reefs. Oikos 123: 829-836

Rizzari JR, Bergseth BJ, Frisch AJ (2015) Impact of conservation areas on trophic intercations between apex predators and herbivores on coral reefs. Conservation Biology 29: 418-429

Additional publications arising during PhD candidature

Frisch AJ, Cole AJ, Hobbs J-PA, **Rizzari JR**, Munkres KP (2012) Effects of spearfishing on reef fish populations in a multi-use conservation area. PLoS ONE 7:e51938

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Rizzari JR, Frisch AJ (2015) Decadal den fidelity of a highly mobile reef lobster. Marine Biodiversity. DOI: 10.1007/s12526-014-0297-1

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How robust are estimates of coral reef shark depletion?

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ORIGINAL PAPER

Diversity, abundance, and distribution of reef sharks on outer-shelf reefs of the Great Barrier Reef, Australia

Justin R. Rizzari · Ashley J. Frisch ·
Katalin A. Magnenat

Conservation Biology

Contributed Paper

Impact of conservation areas on trophic interactions between apex predators and herbivores on coral reefs

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Not worth the risk: apex predators suppress herbivory on coral reefs

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